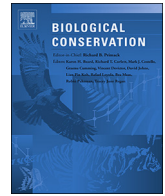




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# Linking ecosystem condition and landscape context in the conservation of ecosystem multifunctionality

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## ABSTRACT

Nature reserves are often implemented to restore the condition of habitats, protect populations of harvested species and to protect, as well as enhance, ecological functions. It is, however, not clear whether and how the spatial context of reserves influences their capacity to promote this ecosystem multifunctionality. We measured how the spatial context of no-take marine reserves and the condition of ecosystems combine to structure animal assemblages and modify rates of two key ecological functions (herbivory, carrion scavenging) in mangrove forests in the Moreton Bay Marine Park, Queensland, Australia. Fish diversity and the abundance of harvested fish species were highest inside reserves, and in mangrove forests nearer to the open ocean and moderate-sized seagrass meadows, and far from coral reefs. The rates of both ecological functions were, however, not elevated inside reserves. The highest rates of carrion scavenging occurred in mangrove forests that were open to fishing, far from the open ocean, and near both large seagrass meadows and coral reefs. Herbivory was highest in mangrove forests that were close to both large seagrass meadows and coral reefs, and with abundant pneumatophores and low mangrove tree canopy cover. We therefore found positive effects of reserves on animal assemblages, but not on ecological functions, and show that ecosystem multifunctionality is not always tightly linked with biodiversity. The results of this study highlight the importance of quantitative conservation goals, and in integrating data on both the ecological condition and spatial context of ecosystems when prioritizing conservation to maximise both biodiversity and ecosystem multifunctionality.

## 1. Introduction

Anthropogenic impacts degrade ecosystem condition and functioning directly through the effects of habitat loss and replacement, and indirectly through overharvesting and changes in biogeochemical processes (Asaad et al., 2017; Halpern et al., 2019). These stressors combine to reduce biodiversity, change the rate and distribution of ecological functions, and reduce the resilience of ecosystems to disturbance (Asaad et al., 2017; Mellin et al., 2016; Roberts et al., 2017). Importantly, they also degrade the provision of ecosystem services, including fisheries, carbon and nutrient sequestration, and recreation (Halpern et al., 2019; Roberts et al., 2017). Nature reserves are often implemented to enhance ecosystem function and services (Gilby et al., 2017; Wiens and Hobbs, 2015) by reducing exposure to particular stressors (Ripple and Beschta, 2007) which allows for the protection of threatened, and economically or functionally important species (Henderson et al., 2019b). Maximising the potential ecological benefits

of reserve networks across this diversity of intended outcomes requires careful design, and the strategic placement of individual reserves (Olds et al., 2016; Salomon et al., 2006).

Designing nature reserves that maximise the protection of biodiversity and the rates of multiple ecological functions, as well as the provision of ecosystem services, could help to improve the ecological and economic benefits of conservation (Munguia-Vega et al., 2018; Taylor et al., 2017). For example, the capacity for ecosystems to recover from disturbance depends on the degree to which multiple ecological functions combine to maintain the condition and structure of habitat forming species and food webs (Alsterberg et al., 2017; Gamfeldt et al., 2008). Higher biodiversity can enhance rates of multiple ecological functions (i.e. processes by ecosystems or species, such as nutrient cycling, which are essential for the capacity of an ecosystem to provide services; De Groot et al., 2002; Hölting et al., 2019), which in-turn can be positively linked to the condition and resilience of ecosystems, and the provision of ecosystem services (i.e. the benefits derived by humans

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from ecosystem functions; Hölting et al., 2019) (Brodie et al., 2018; Manning et al., 2018; Mellin et al., 2016; Topor et al., 2019). The importance of this multifunctionality in ecosystem ecology is widely recognised, but the concept is rarely integrated into conservation planning and this likely detracts from the capacity of reserves to deliver multiple ecological benefits (Gamfeldt et al., 2008; Mellin et al., 2016). The presence, abundance or diversity of species that perform important functions are often used as surrogates when identifying, and prioritizing, perceived hotspots for ecological functioning in conservation (Henderson et al., 2019b; Mumby et al., 2008). The spatial distribution of animals and the manifold ecological functions they perform is frequently structured by the variation in the position, size and shape of ecosystems in landscapes. Several landscape processes, including landscape complementation and landscape supplementation, indicate that patches of habitat that are within closer proximity to one another are able to support a larger population of animals due to greater accessibility to a variety of resources (Dunning et al., 1992). The conservation of multiple species and ecological functions therefore requires adequate protection of this landscape diversity (Alsterberg et al., 2017), so placing reserves to protect multiple features of a landscape is an increasing priority (Gaines et al., 2010; Taylor et al., 2017). Identifying the spatial and environmental variables that most influence the distribution of biodiversity, ecological functions and ecosystem services is therefore pivotal when prioritizing the location of reserves to conserve and maximise ecosystem multifunctionality (Brodie et al., 2018; Salomon et al., 2006; Yabsley et al., 2016).

Coastal ecosystems are impacted by a diversity of human impacts (Halpern et al., 2019). Marine nature reserves can aid in the recovery of coastal ecosystems from some of these impacts by protecting ecosystems from direct degradation (Roberts et al., 2017), helping the recovery of overharvested fish assemblages (Krueck et al., 2017) and restoring the rates of key ecological functions (Mellin et al., 2016; Yabsley et al., 2016). These changes can proliferate through food webs to improvements in the condition of habitats within reserves (Gilby and Stevens, 2014; Mumby et al., 2008). Because coastal ecosystems are comprised of a heterogeneous mix of habitats (e.g. marshes, coral reefs, seagrass meadows and mangrove forests), the importance of strategically placing reserves to maximise ecosystem connectivity is increasingly recognised (Olds et al., 2016; Weeks, 2017). For example, connectivity between mangrove forests and coral reefs is an important predictor of the structure of fish assemblages, rates of ecological functions and coral reef condition in many tropical seascapes, and therefore of the effectiveness of reserves in maximising fish abundance and biomass (Dubuc et al., 2019; Olds et al., 2013). The ability for management to optimise the placement of reserves to not only conserve ecosystems, but also to maximise the rates of multiple ecological functions and ecosystem services in coastal seascapes is increasingly recognised as important (Alsterberg et al., 2017; Gamfeldt et al., 2008; Olds et al., 2013). However, the attributes of ecosystems and seascapes that maximise multifunctionality are yet to be quantified in many systems, and are therefore rarely incorporated into coastal conservation planning (Gilby et al., 2017; Olds et al., 2016; Weeks, 2017).

Mangrove forests are ecologically and economically important coastal ecosystems that have declined globally due to human activities, with losses of as much as 50% in some areas (Bunting et al., 2018; Románach et al., 2018). They are nursery habitats for a diversity of fishes (Sheaves et al., 2015) and marine megafauna (Sievers et al., 2019), attenuate waves and wind from severe storms (Románach et al., 2018), and are important sites for carbon sequestration (Atwood et al., 2017). Consequently, there is an increasing desire to implement reserves to protect mangrove forests (McNally et al., 2011). The distribution of animals, and therefore the ecological functions and services they provide in mangrove forests, is modified by their seascape context, especially in meso- and macrotidal systems where fish that use mangroves must seek alternate subtidal habitats (e.g. coral reefs, seagrasses) at low tide (Igulu et al., 2014; Olds et al., 2012a; Pittman et al., 2004).

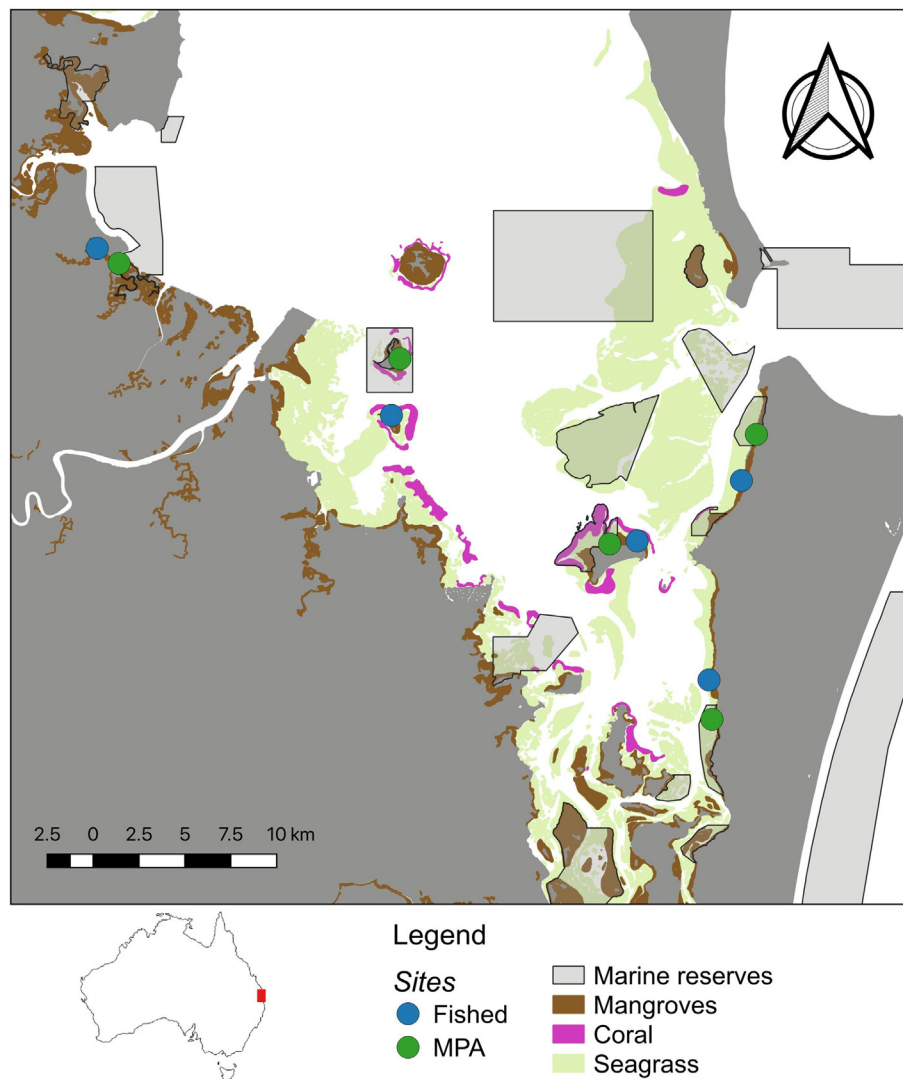
Similarly, the tree species composition, density and complexity of the mangrove forest might affect the habitat value of mangroves for some animals by modifying protection from predation or food availability (e.g. Nagelkerken et al., 2010). Ecological functions that are performed by animals (e.g. herbivory, carrion scavenging, pollination) also play a significant, but often under-recognised role, in maintaining the ecological condition of mangrove forests (Kimirei et al., 2013). For example, herbivorous fish and invertebrates remove algae growing on the prop roots and pneumatophores of mangroves, which facilitates root oxygen exchange and can improve mangrove growth (Cannicci et al., 2008). Dead animal material is also often washed into mangrove forests from the sea by waves and tides, and the consumption of this carrion by scavengers prevents the build-up of rotting carcasses, reducing disease risk and enhancing water quality (Olds et al., 2018; Porter and Scanes, 2015). These two ecological functions (i.e. herbivory and carrion scavenging) are typically performed by different functional groups (i.e. herbivores and scavengers) (Henderson et al., 2019b; Olds et al., 2018), and their spatial distribution in mangrove forests might therefore respond in distinct ways to variation in ecosystem and seascape features, with potential opportunities for conservation occurring where distributions overlap (Alsterberg et al., 2017; Martin et al., 2018). Whilst there is some evidence to suggest that the abundance and diversity of herbivores and scavengers is positively affected by the presence of reserves, few studies have measured how variation in the properties of mangrove forests and the seascape in which they occur combine to modify the benefits of reserves for ecological functions (for examples in other ecosystems, see Jennerjahn et al., 2017; Olds et al., 2012a).

In this study, we tested for effects of nature reserves on fish assemblages, and rates of herbivory and scavenging in mangrove forests by adopting a multi-scale seascape ecology approach and measuring within-patch structure and the composition and spatial configuration of patches. We hypothesised that the abundance and diversity of harvested fish species, and rates of herbivory and scavenging would be higher in protected mangrove forests than in fished mangrove forests. The magnitude of reserve effects was, however, expected to vary with the proximity of mangroves to other fish habitats that provide refugia at low tide (e.g. coral reefs and seagrass), and the habitat attributes of mangroves (e.g. tree density and size). Here, we expected that fish abundance and diversity would be higher with higher habitat connectivity and greater mangrove forest complexity. We also anticipated higher habitat complexity and lower coverage of algae on pneumatophores within reserves through due to increased protection, and subsequent effects on rates of ecological functions.

## 2. Methods

### 2.1. Study region

Fish assemblages and ecological functions were measured in mangrove forests in the Moreton Bay Marine Park (MBMP), which encompasses a large (~3400 km<sup>2</sup>), subtropical embayment in southern Queensland, Australia (~27°25S, 153°23E) (Fig. 1). MBMP is a multiple-use marine park with 16% of the bay designated as no-take reserves. Hydrodynamic influences are both oceanic, originating from the open sea to the north and east, and estuarine, originating from four major rivers that discharge into the south and west, resulting in strong east-west and north-south water quality gradients. Proximity to the open ocean is therefore a reliable predictor of water quality in the region (Davis et al., 2014; Henderson et al., 2017b; Maxwell et al., 2014). The seascape is comprised of a heterogeneous mix of habitats, principally mangroves, seagrasses, and coral reefs among a matrix of sandy and muddy substrates (Henderson et al., 2019b; Kenyon et al., 2018). We surveyed ten sites, five in no-take reserves (i.e. no extractive industries of any kind permitted) and five that were open to fishing; these were chosen to represent a broad range of seascape contexts and positions along the water quality gradient in Moreton Bay (Fig. 1).



**Fig. 1.** Map of study sites and focal ecosystems in Moreton Bay, Australia.

Moreton Bay is a significant site for both recreational and commercial fishing, so all sites open to fishing are likely subject to significant extraction by fishers (Pascoe et al., 2014; Webley et al., 2015). All of the reserves that we surveyed have been in place since 2009, except for the Peel Island reserve which has been in place since 2003. Surveys were conducted in the austral winter of 2019. Moreton Bay has a usual tidal range of between 1.5 and 2.5 m, and most mangroves along the seaward edge are inundated for approximately half of the day. We intentionally placed reserve and non-reserve sites in similar seascape contexts across Moreton Bay in order for these to share similar seascape attributes of mangroves, thereby allowing us to most effectively quantify whether the reserves were influencing changes fish community structure and enhancing functions they perform across the diverse seascape and range of habitats conditions present.

## 2.2. Fish assemblage surveys

We deployed 10 baited remote underwater video stations (BRUVS) to sample fish assemblages at each site (for 100 BRUVS replicates in total, and  $n = 100$  in analyses). BRUVS are made of a GoPro HD video camera secured to a 5 kg weight with a 1 m length of PVC pipe that holds a mesh bait bag containing 500 g of pilchards *Sardinops sagax*. The first BRUVS was deployed randomly at each site, with subsequent BRUVS placed along the mangrove fringe at 200 m intervals. This

ensures spatial independence of each BRUVS sample as fish are unlikely to be encountered on more than one BRUVS deployment during the one hour deployment period (Gilby et al., 2017; Henderson et al., 2017a). We placed BRUVS along the edge of the mangrove forest at each site because this location is the area of highest utilisation by fish (Dubuc et al., 2019; Sheaves et al., 2016). BRUVS were deployed within two hours of high tide to ensure maximum accessibility to the mangroves by fish (Harvey et al., 2007; Henderson et al., 2019a; Olds et al., 2012a). Fish assemblages were quantified from the resulting videos using the standard *MaxN* statistic (the maximum number of individuals identified of each species in any one frame within each video). Whilst BRUVS have the ability to attract a large number of predatory and scavenging fish species, the use of bait doesn't decrease the abundance of herbivorous or omnivorous fish (Harvey et al., 2007).

## 2.3. Ecological function surveys

Rates of scavenging were quantified at each site by deploying three pilchards of known weight (weighed using digital scales to the nearest 0.01 g) to the outside of BRUVS bait bags, which were weighed again following 1 h of BRUVS deployment (following Olds et al., 2018). Scavenging is indexed as a percent loss of the original weight of pilchards for each BRUVS deployment. The proportion of carrion consumed by each scavenging species was identified using the BRUVS

videos by visually estimating from BRUVS videos the amount of carrion consumed by each species as a percent of the total carrion lost. Previous studies using the same method have shown no significant reduction in pilchard weight on scavenging assays where no consumption was recorded (Olds et al., 2018).

Herbivory was quantified at each site by deploying mangrove pneumatophores covered in *Catenella nipae*; a red alga commonly found growing in mangrove forests in Moreton Bay. *Catenella* is readily consumed by a variety of herbivores in Moreton Bay (Davis et al., 2014; Gilby et al., 2015), and has been used to index herbivory rates in multiple ecosystems in Moreton Bay (Gilby et al., 2015; Henderson et al., 2019b). Pneumatophores covered in *Catenella* were collected from Cleveland on the western coastline of Moreton Bay, with deployments occurring at random positions along the mangrove fringe between the first and last BRUVS deployment at each site. Deployments were constructed by attaching twelve replicate pneumatophores across two randomly placed 10 m transects at each site and deployed for 72 h. *Catenella* was weighed before and after deployment using 60 g Persola spring scales.

#### 2.4. Environmental variables

We quantified correlations between the mangrove condition metrics, fish assemblages and ecological functions in mangrove forests with three classes of environmental variables (Table 1). Firstly, we quantified effects of marine reserves on dependent variables. Secondly, we quantified effects of the seascape context on dependent variables by

measuring the proximity and area of adjacent marine ecosystems. Proximity to coral reefs, open ocean and seagrass meadows from each deployment was calculated within QGIS following the contour of the coast. The area of mangroves, coral reefs, and seagrass meadows within a 500 m buffer around each site was quantified in QGIS by clipping a shapefile of each habitat using 500 m buffers, and calculating the total extent of the resulting areas for each buffer in m<sup>2</sup>. A 500 m buffer was chosen as the focal scale because it has been shown to capture the daily home ranges of common mangrove and coral reef fish species in Moreton Bay (Olds et al., 2012a). Finally, we indexed the condition of mangrove forests by recording the number and species of each tree, tree diameter (at both the base and breast height) and canopy height and cover in a 10 × 10 m quadrat directly adjacent to the position of each BRUVS deployment. We also measured the cover of benthic algae and number of mangrove pneumatophores in four 1 × 1 m quadrats, which were randomly placed within the broader 10 × 10 m quadrats. Two variables, mangrove tree density and the extent of nearby mangrove forests (i.e. mangrove connected area), were removed from analyses as they correlated positively with the distance of the site to the nearest opening to the open ocean (> 0.7 R).

#### 2.5. Data analyses

We used a ManyGLM in the *mvabund* package of R (Wang et al., 2012) to identify the environmental variables that best correlate with variation in the composition of fish assemblages at the edge of mangrove forests, and the fish species that best correlated with these

**Table 1**  
Environmental metrics, their definitions, data sources and hypotheses.

Environmental metric	Definition	Hypotheses
Reserve status	Whether the site is positioned in a no-take marine reserve or fished area.	Sites within reserves will have a higher abundance and diversity of fish assemblages due to lower fishing and boating activities.
Seascape context		
Distance to seagrass, coral and ocean	Distance (m) from BRUVS deployments to the nearest seagrass, coral reef and ocean opening (point in centre of ocean mouth) (Queensland Government, 2019).	Increased connectivity of mangrove forests to seagrass, coral reefs and ocean will result in a greater abundance and diversity of fish assemblages because they contain species from both habitats.
Seagrass, coral and mangrove area	Area (m <sup>2</sup> ) of seagrass, coral reef and mangrove forest within a 500 m buffer of each BRUVS deployment (Queensland Government, 2019).	Greater areas of seagrass, mangroves and coral reefs will result in a greater abundance and diversity of fish assemblages in mangrove forests because they contain species from both habitats.
Mangrove connected area	Area (m <sup>2</sup> ) of unbroken mangrove forest adjacent to each BRUVS deployment (Queensland Government, 2019).	Greater area of connected mangroves will result in a greater abundance and diversity of fish assemblages in mangrove forests.
Mangrove condition metrics		
Canopy height	Highest point (m) of the mangrove trees within a 10 × 10 m quadrat at each BRUVS deployment site.	Greater canopy height might provide protection for prey species from predation, and might indicate larger or older mangroves trees, thereby resulting in an increased abundance and diversity of fish assemblages in mangrove forests.
Canopy cover	Mangrove canopy cover (%) within a 10 × 10 m quadrat at each BRUVS deployment site.	Greater canopy cover might provide protection for prey species, resulting in an increased abundance and diversity of fish assemblages in mangrove forests.
Mangrove species and abundance	The number of each mangrove species within a 10 × 10 m quadrat at each BRUVS deployment site.	The density and type of mangrove trees will change the abundance and diversity of fish assemblages by increasing protection and modifying habitat complexity. For example, a greater abundance of orange mangroves will create further protection for smaller species due to their more intricate prop roots.
Mangrove measurements	Diameter at breast height (DBH) and diameter at base (cm) of up to 10 randomly selected mangroves of each species within the 10 × 10 m quadrat at BRUVS deployment site.	Smaller, more abundant base diameters will create a more complex habitat, modifying the abundance and diversity of fish assemblages. However, larger base diameters will provide greater protection and feeding opportunities.
Pneumatophores	Average number of pneumatophores counted within four randomly placed 1 m × 1 m quadrats within the broader 10 × 10 m quadrat at each BRUVS deployment site.	Greater number of pneumatophores will increase potential sites for algal growth and will result in mangrove forests with a greater complexity, thereby increasing abundance and diversity of fish assemblages.
Algae cover	Average cover of algae (in %) within four randomly placed 1 × 1 m quadrats within the broader 10 × 10 m quadrat at each BRUVS deployment site.	Higher coverage of algae in mangrove forests might prevent some species from entering the forest, or from accessing benthic prey. Conversely, greater coverage of algae reduces the novelty of our algae deployments, affecting the rate of herbivory.
Crab holes	Average number of crab holes counted within four randomly placed 1 m × 1 m quadrats within the broader 10 × 10 m quadrat at each BRUVS deployment site.	Crab holes are a proxy for the abundance of small invertebrates in soft sediment systems, so higher density of crab holes will provide greater feeding opportunities for fish in mangrove forests.

variables. We also used a ManyGLM to examine how mangrove condition attributes varied spatially across Moreton Bay. Best fit ManyGLMs were identified using reverse stepwise simplification using Akaike information criterion (AIC), and visualised using non-metric multidimensional scaling ordinations. We further interrogated relationships between environmental variables from the best fit ManyGLM for fish assemblages, and fish species richness, the abundance of key species (as identified by the ManyGLM) and harvestable fish abundance (calculated as the sum of the MaxN of species captured in commercial and recreational fisheries in the region) using generalised additive models (GAMs) in the mgcv package of R (Nash et al., 2016). We minimised model overfitting by fitting GAMs with four polynomial links or fewer ( $k = 4$ ). We also used GAMs to identify environmental variables that best explained rates of carrion scavenging and herbivory. Best fit GAMs were also identified using reverse stepwise simplification.

### 3. Results

#### 3.1. Habitat condition

The composition and habitat condition of mangrove forests were best explained by the distance of sites from the ocean ( $\chi^2 = 9.42$ ,  $p = 0.001$ ) and coral reefs ( $\chi^2 = 9.82$ ,  $p = 0.001$ ), and the area of mangroves ( $\chi^2 = 6.91$ ,  $p = 0.001$ ) and coral reef nearby ( $\chi^2 = 352.68$ ,  $p = 0.001$ ) (Fig. 2). We found a higher density of mangrove trees, predominantly grey mangroves, and a higher density of crab holes and pneumatophores at sites nearer to the ocean and coral reefs and with greater mangrove area (Fig. 2). Mangrove trees with a larger diameter at breast height occurred predominantly at sites with a larger extent of coral nearby. Greater algae cover within mangrove forests and greater abundance of orange mangroves were found at sites further from coral reefs (Fig. 2).

#### 3.2. Fish assemblages

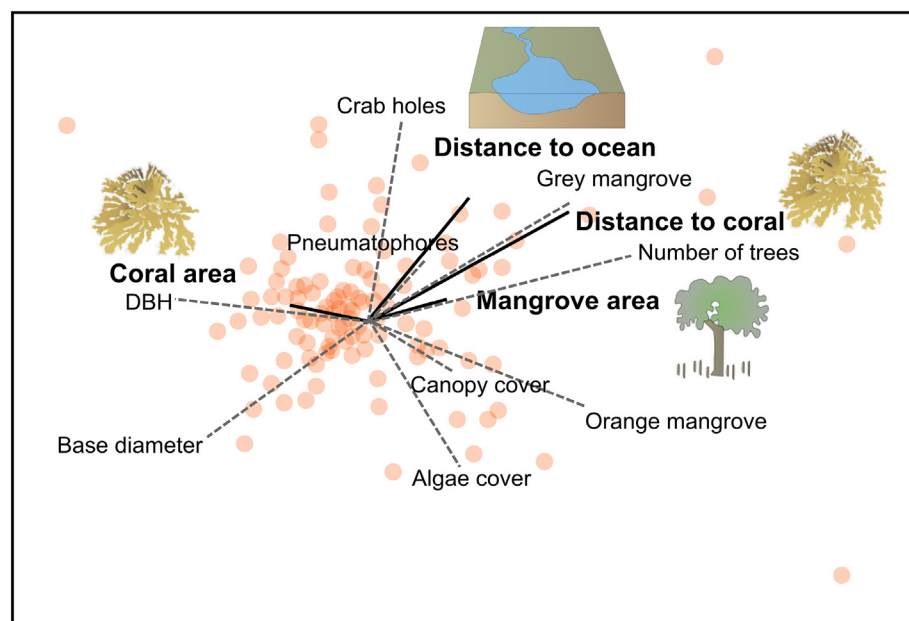
Reserve effects were positive for each of our fish assemblage metrics, however the scale of these positive effects of reserves was mediated by seascape context. The composition of fish assemblages was strongly influenced by reserve status ( $\chi^2 = 7.85$ ,  $p = 0.001$ ), the distance of sites to the open ocean ( $\chi^2 = 9.37$ ,  $p = 0.002$ ) and coral reefs ( $\chi^2 = 7.87$ ,  $p = 0.002$ ), and the area of seagrass nearby ( $\chi^2 = 8.83$ ,

$p = 0.001$ ) (Fig. 3). We found more yellowfin bream *Acanthopagrus australis* (276% higher in reserves), sand whiting *Sillago analis* (458% higher in reserves), estuary perchlet *Ambassis marianus* (242% higher in reserves) and common hardyhead *Atherinomorus vaigiensis* (252% higher in reserves) in reserves than at fished sites. By contrast, only estuary rays *Hemirhamphys fluviorum* were more abundant at fished sites. The distribution of yellowfin bream was the most significant indicator of these spatial variations within the assemblage composition. Yellowfin bream were in higher abundance at reserve sites that had less seagrass nearby, and that were at intermediate distance from both coral reefs and the open ocean (Fig. 3).

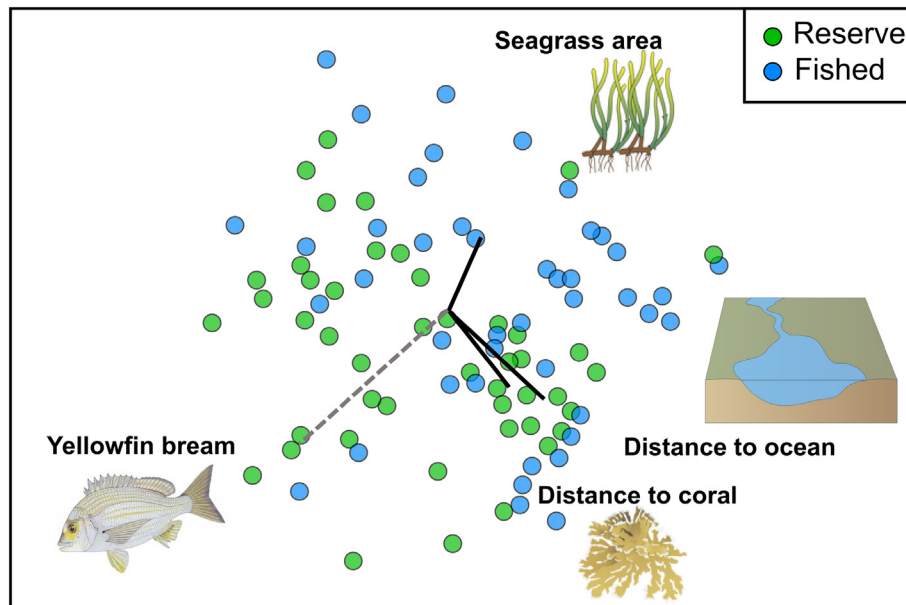
Species richness was highest in reserves ( $\chi^2 = 8.75$ ,  $p = 0.003$ ) and nearer to the open ocean ( $\chi^2 = 13.10$ ,  $p < 0.001$ ) (Fig. 4A). The abundance of harvested fish species was also highest in reserves ( $\chi^2 = 73.86$ ,  $p < 0.001$ ), nearer to the open ocean ( $\chi^2 = 75.27$ ,  $p < 0.001$ ), and at sites with intermediate area of seagrass nearby ( $\chi^2 = 14.65$ ,  $p = 0.007$ ) further from coral reefs ( $\chi^2 = 13.14$ ,  $p = 0.004$ ) (Fig. 4B). The abundance of yellowfin bream followed patterns for harvested fish abundance, and were most abundant in reserves ( $\chi^2 = 53.37$ ,  $p = 0.001$ ), nearer to the open ocean ( $\chi^2 = 32.14$ ,  $p < 0.001$ ) and with lower seagrass area nearby ( $\chi^2 = 22.84$ ,  $p < 0.001$ ) (Fig. 4C).

#### 3.3. Ecological functions

Rates of scavenging and herbivory were not positively affected by reserves, and were best explained by combination of seascape context (distance to ocean and coral reefs and area of seagrass nearby) and habitat variables (canopy cover and number of pneumatophores). Carrion was consumed by five fish species: estuary rays *Hemirhamphys fluviorum* (53% biomass consumed); yellowfin bream (18%); nervous sharks *Carcharhinus caudatus* (16%); brown-banded bamboo sharks *Chiloscyllium punctatum* (11%); and toadfish *Marilyna pleurosticta* (2%). Rates of carrion scavenging were higher in mangroves that were open to fishing ( $\chi^2 = 31.45$ ,  $p < 0.001$ ), far from the open ocean ( $\chi^2 = 230.60$ ,  $p < 0.001$ ), close to coral reefs ( $\chi^2 = 35.05$ ,  $p < 0.001$ ) and at sites with both small and large areas of seagrass nearby ( $\chi^2 = 223.34$ ,  $p < 0.001$ ) (Fig. 4D). Scavenging was dominated by yellowfin bream and nervous shark at sites with a small area of seagrass nearby ( $< 130,000 \text{ m}^2$ ). By contrast, scavenging was dominated by estuary ray at sites with a large area of seagrass nearby



**Fig. 2.** Multi-dimensional scaling ordination (MDS) of mangrove attributes. Pearson vector overlays represent spatial variables from the best fit ManyGLM (black vectors) and mangrove attributes that correlate significantly with the best fit model (grey vectors). DBH = tree diameter at breast height. Each point shows an individual BRUVS deployment site.



**Fig. 3.** Multi-dimensional scaling ordination (MDS) of fish assemblages between reserves and fished sites. Pearson vector overlays represent variables from the best fit ManyGLM (black vectors) and species that correlate significantly with the best fit model (grey vector). Each point shows an individual BRUVS deployment site.

(> 130,000 m<sup>2</sup>) within reserves. Rates of herbivory were higher in mangroves that had more seagrass nearby ( $F = 24.56$ ,  $p < 0.001$ ), were close to coral reefs ( $F = 4.19$ ,  $p = 0.042$ ), and at sites with both low canopy cover ( $F = 16.02$ ,  $p < 0.001$ ) and high pneumatophore density ( $F = 10.38$ ,  $p < 0.001$ ) (Fig. 4E).

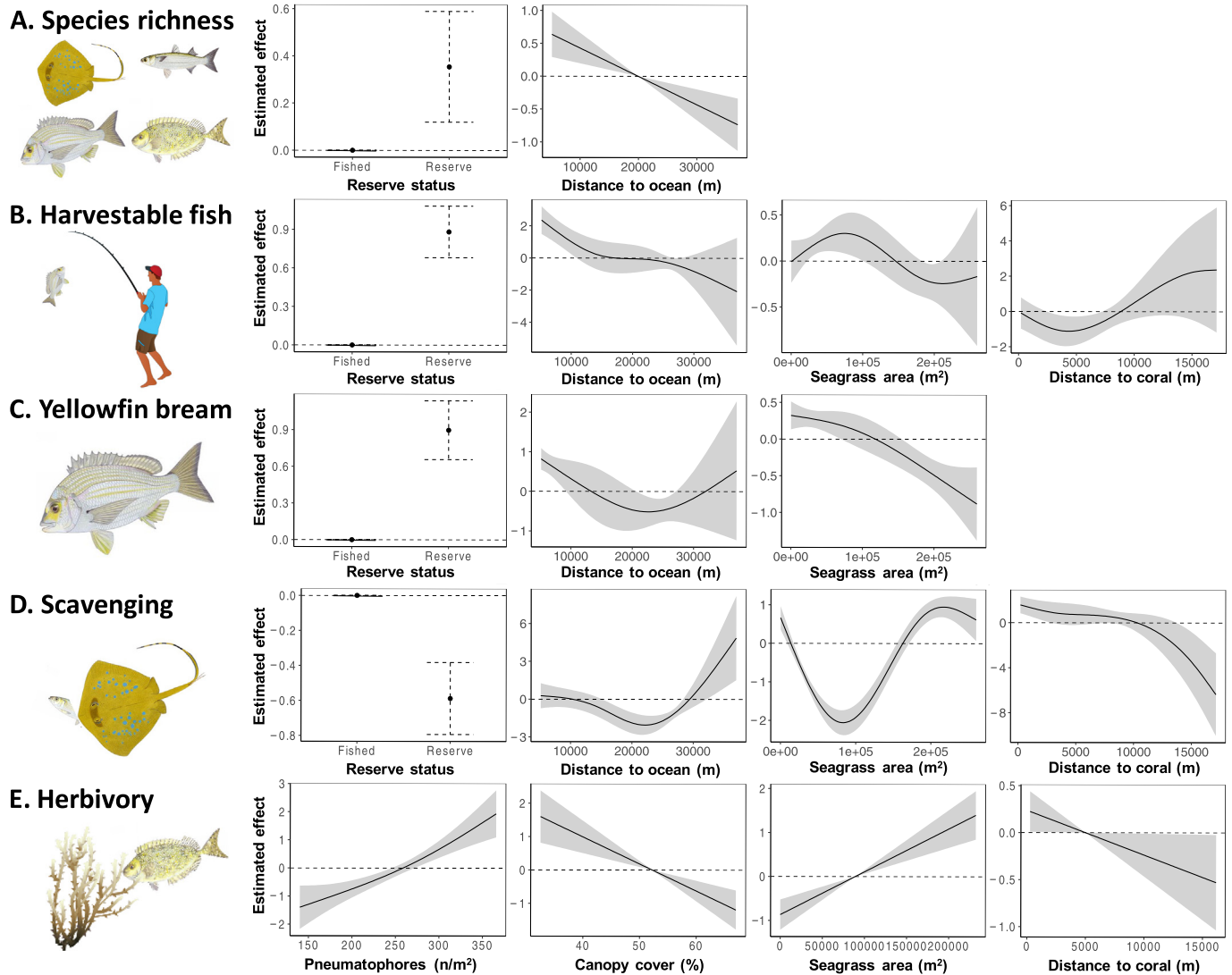
#### 4. Discussion

Nature reserves that maximise the conservation of habitats and biodiversity can protect and restore ecological functions and enhance the provision of ecosystems services (Halpern et al., 2013). However, managers rarely have information on the variables that modify the distribution of multiple ecological functions, and hence can rarely consider ecosystem multifunctionality in conservation planning (Gamfeldt et al., 2008). We show that marine reserves, seascape context and the condition and structure of habitats jointly modify the abundance and diversity of fish assemblages and the rates of two ecological functions in mangrove forests in Moreton Bay. Fish species richness, the abundance of harvested fishes, and several key fish species were greater inside reserves. Implementing reserves to protect mangrove forests can, therefore, yield significant benefits for fish assemblages. Positive reserve effects for fish were modified by the seascape context of reserve locations, especially connectivity with the open ocean, seagrass meadows and coral reefs. By contrast, rates of scavenging were higher at sites that were open to fishing and farther from the open ocean, and rates of herbivory were modified by both seascape context (connectivity with seagrass and coral reefs) and the habitat structure of the mangrove forest (i.e. pneumatophore density and canopy cover). This juxtaposition of reserve effects on fish assemblages and ecological function suggests that careful spatial prioritization might be required to optimise conservation outcomes for both ecological structure and function. In this case, due to these being highly complex systems with multiple spatial drivers of fauna, flora and function, maximising diversity, abundance, function and services in one location is likely difficult. However, our results show clearly that it is useful to have empirical data to describe the ecosystem and seascape attributes that are tightly linked to spatial variation in both biodiversity and ecological functions in order to best protect, and potentially enhance, all aspects of multifunctionality across seascapes.

Nature reserves are often implemented to protect and improve

biodiversity and habitat condition (Wiens and Hobbs, 2015), and the principle objective for reserves in coastal seascapes is to counteract the effects of harvesting fish (Munguia-Vega et al., 2018; Roberts et al., 2003). This is also often extended to enhancing the rate of key ecological functions in reserves, such as herbivory on coral reefs (Mumby et al., 2006; Nash et al., 2016). Our results show that reserves can deliver substantial benefits for mangrove forests by enhancing the abundance (especially of harvestable fishes) and diversity of fish assemblages. These reserve effects were strongest for yellowfin bream; an important target of commercial and recreational fisheries in this region (Webley et al., 2015). Yellowfin bream are abundant in many ecosystems in southeast Queensland, where they are also typically the dominant scavenger. Whilst we did not find positive effects of reserves on scavenging rates, the high abundance of yellowfin bream in reserves suggests that protected mangroves still have a high potential for carrion consumption, and might experience high scavenging at other times. These positive results for fish assemblages suggest that placing marine reserves to conserve mangroves for the purposes of enhancing fish and fisheries should be considered more often, irrespective of uncertainties around reserve benefits in these ecosystems which are inundated for only part of the day in many regions of the world.

The position of reserves in seascapes can affect their capacity to deliver conservation outcomes (Olds et al., 2016). Reserves positively influenced the abundance and diversity of fish communities within mangrove forests, however, the scale of these benefits was modified by the connectivity of sites with seagrasses, coral reefs and the open ocean. Distance to ocean was collinear with tree density and area of connected mangrove forest, thereby indicating that the structural complexity of mangrove forests (i.e. tree density) may have also modified fish community structure along this gradient (Nagelkerken et al., 2010). These results align with the other studies on the effectiveness of marine reserves across seascapes both in the Moreton Bay Marine Park (Davis et al., 2014; Henderson et al., 2017b) and beyond (Mosquera et al., 2000; Olds et al., 2016). Our results therefore lend further support to the notion that marine reserves can be placed strategically within seascapes to maximise multifunctionality. Designing reserves to account for connectivity between complementary habitats and the condition of those ecosystems should also consider strategically placing reserves to cover impact gradients. In this study, we measured reserve performance across a water quality impact gradient which has



**Fig. 4.** Generalised additive model (GAM) partial plots for A) species richness, B) harvested fish abundance, C) yellowfin bream abundance, and rates of D) scavenging and E) herbivory against variables from the best fit model.

documented effects on the condition of ecosystems and the composition of fish assemblages (Maxwell et al., 2014). Distance to ocean correlates with water quality variables within this region (Davis et al., 2014; Henderson et al., 2017b; Maxwell et al., 2014). Whilst the effect of runoff events was not a focus of this study, the effects of distance to ocean on fish assemblage abundance and diversity indicates the potential importance of these disturbance gradients over longer timeframes (i.e. years). Further studies are required within mangrove forests to identify how pulse events from estuaries might modify the consistency of the effects found here. Combined, our findings highlight that the spatially heterogeneous distribution of ecosystem services and ecological functions demands quantitative support for reserve design and placement in order to maximise conservation outcomes.

An important goal of conservation planning is to protect representative samples of ecosystems across landscapes (Margules and Pressey, 2000). These plans are often implemented using the assumption that areas of a particular habitat are equivalent in terms of their condition and/or values for animals (Salomon et al., 2006). We established that some attributes of mangrove forest complexity (i.e. pneumatophore density and canopy cover) significantly modify the rates of key ecological functions, meaning that understanding the distribution of these attributes across seascape is vital. Our results show that there are clear spatial patterns in the attributes of mangrove forests, and that

these attributes affect fish species and ecological functions in different ways. Here, mangrove complexity and condition as measured by number of crab holes, higher number of pneumatophores and the density, size and composition of mangrove trees was correlated with distance to ocean, distance to coral and mangrove area. These patterns are likely the result of the hydrological regimes and level of human impacts at particular sites. For example, sites in narrow estuaries might have a greater supply of propagules and so have a greater density of predominantly smaller trees and saplings. Propagules at sites with larger trees would have a lower likelihood of taking root and growing given the presence of dense tree canopies and root systems restricting their growth (Tamai and Iampa, 1988). Sites with larger trees in this study were often in areas nearer to the open ocean, and therefore further away from human disturbances. Most often, habitat complexity is correlated with greater fish abundance and diversity in coastal seascapes because of the increased opportunities for feeding and sheltering that are associated with a greater diversity of both ecosystems and habitats (Davis et al., 2014; Henderson et al., 2019b). Responses for individual species, however, may differ according to their individual requirements (Pittman et al., 2004) which could be an important focus of future research when focusing on particular species for fishery purposes. Consequently, our results highlight the importance of considering the structural attributes of mangrove forests, like tree density

and size, in strategic spatial conservation prioritization. Habitat condition measures have rarely been incorporated in reserve design, but their significance are gaining traction in the conservation literature (Berglund et al., 2012).

In this study, we found that different suites of environmental variables correlated with rates of carrion scavenging and herbivory. Reserve status did not have a positive effect on the rates of carrion consumption and we found that carrion scavenging was linked to the distribution of a single species, the estuary ray, which consumed carrion only in areas open to fishing (Inger et al., 2016; Olds et al., 2018). The estuary ray is a listed vulnerable species so is therefore not a harvested species in this region (Webley et al., 2015). Conversely, yellowfin bream, a heavily-harvested species, predominantly consumed carrion in reserves. Therefore, yellowfin bream was functionally dominant over estuary rays when fishing was low. This might indicate that there is a competitive release for threatened rays outside reserves, but this hypothesis requires further testing. Spatial segregation of the effects of yellowfin bream and estuary rays, and their differences in harvest rates in the region highlights the potential for fishing to modify the rate, spatial distribution of ecological functions in coastal seascapes. This dominance of the function of carrion consumption function by few, or single species in different contexts has been found in several previous studies (Inger et al., 2016; Olds et al., 2018). Herbivory was correlated with variation in mangrove canopy cover and pneumatophore density. Mangrove forests with a lower canopy cover have greater light penetration, resulting in greater algae growth (Verweij et al., 2006). A higher density of pneumatophores also provides a greater surface area for algae to attach (Melville and Pulkownik, 2007). Combined, these variables influence the cover of algae growing in forests, and therefore the abundance of herbivorous species (Nagelkerken et al., 2008; Verweij et al., 2006). Greater connectivity with surrounding habitats (i.e. coral reefs or seagrass) resulted in a greater rate of herbivory within mangrove forests. This is usually thought to be due to migration of herbivorous fishes from reefs to mangroves during high tide (Davis et al., 2014; Olds et al., 2012a), however, we recorded only very low abundance of potential grazing fish on our BRUVS in this study. Invertebrate grazers (like gastropods, amphipods and brachyurans) were therefore likely responsible for the majority of the algae consumption we measured, and they are not harvested in any fisheries in the region, so their influence on herbivory could conflate any potential reserve effects on the consumption of algae by harvested fishes (Ebrahim et al., 2014). Future studies that quantify more explicitly the roles of these different herbivores (through caging experiments or the like) are therefore crucial to understanding the type and distribution of species that perform this important function in mangrove forests. Whilst different species dominated the functions of carrion scavenging and herbivory, the spatial distribution of these ecological functions was influenced by similar seascape variables (Martin et al., 2018). Mangrove forests that were near large seagrass meadows and close to coral reefs supported higher rates of both ecological functions, which suggests that seascape context is likely to be a pivotal feature when optimising reserve design for ecosystem multifunctionality (Olds et al., 2012b).

Mangrove forests provide a suite of benefits for people and animals, but are under significant threat from human activities (Romañach et al., 2018). In this study, we show that mangrove forests protected by reserves have fish assemblages that are more diverse, and contain a higher abundance of species harvested in fisheries than sites that were open to fishing. Our results follow the findings of a meta-analysis which found that fish abundance were on average 3.7 times higher in reserves compared to outside reserves (Mosquera et al., 2000). We suggest that reserves should be increasingly considered as potential solution to overcome the threats facing mangrove forests globally. Maximising the capacity of reserves to deliver multiple ecological benefits (e.g. for biodiversity, ecological functions and ecosystem services) will, however, require systematic planning to identify and select locations for reserves with optimal combinations of mangrove and seascape-scale

features that support ecosystem multifunctionality. Given the importance of mangroves as nurseries for many fish species, future studies could investigate whether lift history stage, fish size, or species biomass may change with the implementation of no-take reserves in mangrove forests. Our findings offer new insights into how we can improve conservation actions globally, beyond only mangrove forests, by identifying the spatial and habitat variables that drive various benefits that people seek to enhance by implementing reserves. Further, our results highlight the importance of considering the structural attributes of ecosystems, like tree density and size, in strategic spatial conservation prioritization. Consequently, reserves must be planned using explicit conservation goals, especially with respect to the aspects of multifunctionality that are most desired, and placed and prioritised using quantitative information from the region of interest.

#### CRedit authorship contribution statement

**Lucy A. Goodridge Gaines:** Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft. **Andrew D. Olds:** Conceptualization, Methodology, Supervision, Writing - review & editing. **Christopher J. Henderson:** Conceptualization, Methodology, Writing - review & editing. **Rod M. Connolly:** Conceptualization, Writing - review & editing. **Thomas A. Schlacher:** Conceptualization, Writing - review & editing. **Tyson R. Jones:** Methodology, Investigation, Writing - review & editing. **Ben L. Gilby:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Supervision, Funding acquisition.

#### 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.

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