

# Resource type influences the effects of reserves and connectivity on ecological functions

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## Summary

1. Connectivity is a pivotal feature of landscapes that affects the structure of populations and the functioning of ecosystems. It is also a key consideration in conservation planning. But the potential functional effects of landscape connectivity are rarely evaluated in a conservation context.

2. The removal of algae by herbivorous fish is a key ecological function on coral reefs that promotes coral growth and recruitment. Many reef herbivores are harvested and some use other habitats (like mangroves) as nurseries or feeding areas. Thus, the effects of habitat connectivity and marine reserves can jointly promote herbivore populations on coral reefs, thereby influencing reef health.

3. We used a coral reef seascape in eastern Australia to test whether seascape connectivity and reserves influence herbivory. We measured herbivore abundance and rates of herbivory (on turf algae and macroalgae) on reefs that differed in both their level of connectivity to adjacent mangrove habitats and their level of protection from fishing.

4. Reserves enhanced the biomass of herbivorous fish on coral reefs in all seascape settings and promoted consumption of turf algae. Consumption of turf algae was correlated with the biomass of surgeonfish that are exploited outside reserves. By contrast, both reserve status and connectivity influenced herbivory on macroalgae. Consumption of macroalgae was greatest on fished reefs that were far from mangroves and was not strongly correlated with any fish species.

5. Our findings demonstrate that landscape connectivity and reserve status can jointly affect the functioning of ecosystems. Moreover, we show that reserve and connectivity effects can differ markedly depending on resource type (in this case turf algae vs. macroalgae). The effectiveness of conservation initiatives will therefore depend on our ability to understand how these multiple interactive effects structure the distribution of ecological functions. These findings have wider implications for the spatial conservation of heterogeneous environments and strengthen the case that the impact of conservation on ecosystem functioning is contingent on how reserves are positioned in landscapes.

**Key-words:** Australia, coral reef, ecological functioning, fish, landscape ecology, mangrove, resource type, spatial conservation

## Introduction

Fluxes of organisms, materials and energy link the structure and functioning of ecosystems across landscapes

(Loreau, Mouquet & Holt 2003; Hyndes *et al.* 2014). This connectivity is critical for the persistence of all populations and assemblages (Baguette *et al.* 2013; Kool, Moilanen & Treml 2013) and integrates terrestrial, freshwater and marine communities (Knight *et al.* 2005; Huijbers *et al.* 2015). It helps sustain biodiversity and underpins

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the spatial distribution of essential ecological functions (e.g. propagule dispersal, carrion consumption, predator–prey interactions), the structure of food webs and the capacity of ecosystems to resist or recover from disturbance (Lundberg & Moberg 2003; Massol *et al.* 2011; Bernhardt & Leslie 2013). Consequently, connectivity is now a key consideration for conservation planning (Rudnick *et al.* 2012; Olds *et al.* 2015).

Conservation areas (e.g. national parks, marine reserves) can also modify the functioning of ecosystems and are now widely implemented for this purpose (Mace 2014). Functional effects of conservation occur when numbers of exploited consumers increase in the absence of harvesting pressure (Ritchie & Johnson 2009; Edgar *et al.* 2014) and exert strong top-down effects, which alter the abundance, behaviour and feeding ecology of their prey (Ripple *et al.* 2014). This effect of conservation on species interactions can modify ecological functions (e.g. predation and herbivory) that structure the dynamics of species assembly and alter the composition of basal communities, with ecological outcomes dependent on the biology of species that are released from harvesting pressure and the type of resources they consume (Pace, Carpenter & Kitchell 1999; Estes *et al.* 2011). Landscape composition and connectivity affect the distribution, abundance and movement of consumers in reserves, as they do elsewhere, modifying species composition and succession in habitat-forming communities on land (Fortin *et al.* 2005) and at sea (Olds *et al.* 2012a). Thus, it is a common contention in the fields of landscape ecology and conservation biology that connectivity and nature reserves may exert joint effects on the ecological functions that link consumers to the spatial structure of their environments (Bengtsson *et al.* 2003; Massol *et al.* 2011; Pittman & Olds 2015). But the effects of connectivity and landscape composition on ecosystem functioning are rarely considered by studies that evaluate reserve effectiveness (*sensu* Cumming 2011; Olds *et al.* 2015).

In coastal seascapes, the spatial configuration of coral reefs, seagrass meadows and mangrove forests can structure the distribution and movement of organisms (reviewed by Boström *et al.* 2011; Berkström *et al.* 2012; Igulu *et al.* 2014) and affect the performance of marine reserves (Nagelkerken, Grol & Mumby 2012; Olds *et al.* 2013). These effects of seascape connectivity on mobile consumers and herbivores can also modify the composition of seafloor habitats in reserves (Pittman & Olds 2015). For example, herbivorous fish perform an important ecological function on coral reefs: by consuming algae that would otherwise overgrow corals, they help to maintain reefs in a state of coral dominance (Edwards *et al.* 2014; Vergés *et al.* 2014). By feeding on different algal resource types, herbivorous fishes may help reefs to both resist and recover from disturbance. Grazers (e.g. parrotfish and surgeonfish) scrape low-profile turf algae from corals and may help to prevent reefs from being overgrown by algae, whereas browsers (e.g. rabbitfish)

remove established macroalgae from reefs, which may help them recover from algal dominance (Hughes *et al.* 2007). Certain herbivorous reef fish also utilize mangroves as juvenile nurseries or as foraging areas and may thus be more abundant on reefs that are closer to mangroves, in both the Caribbean Sea (Mumby & Hastings 2008) and western Pacific Ocean (Olds *et al.* 2013; Davis *et al.* 2014). Furthermore, inshore coral reefs that are both close to mangroves and protected in marine reserves can support a greater biomass and species richness of herbivorous fish than reefs that are open to fishing (Olds *et al.* 2012a). These joint effects of mangrove connectivity and marine reserves influence the establishment of coral and algae on coral reefs, but the functional mechanism underpinning this effect has not been quantified.

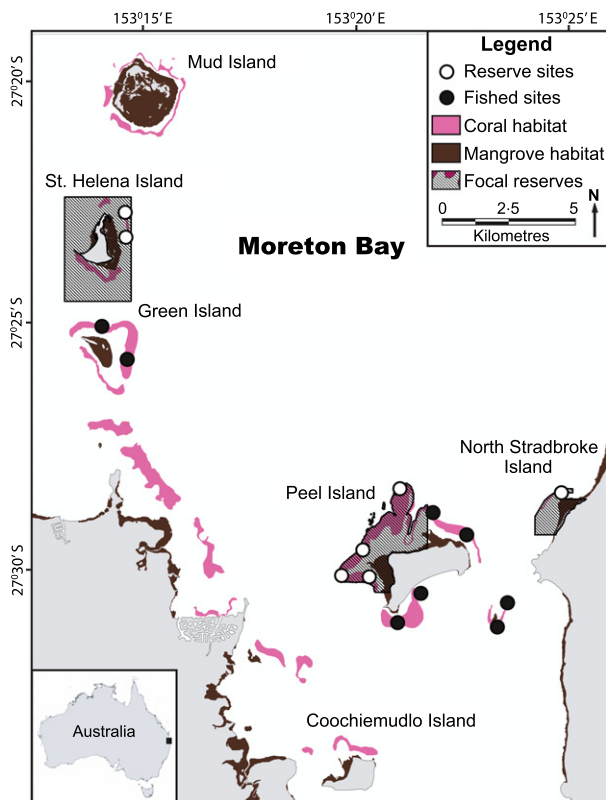
We use inshore coral reef seascapes in the Moreton Bay Marine Park, eastern Australia, as a model system to examine the potential for combined effects of landscape connectivity and conservation on ecological functions. In Moreton Bay, herbivorous fish migrate tidally from coral reefs to adjacent mangroves and seagrass, and reefs that are both near mangroves and protected in marine reserves support more herbivorous fish and experience greater coral recruitment than similar fished reefs (Olds *et al.* 2012a; Davis *et al.* 2014). Reefs that are protected in marine reserves have also been shown to recover more quickly following the impact of extreme floods (Olds *et al.* 2014a). This interdependence of spatial configuration and protection status suggests that mangrove–reef connectivity and reserve protection may shape key ecological functions on local reefs. We test whether connectivity between habitats shapes a key ecological function (herbivory on turf and macroalgae) on coral reefs and examine whether this effect is contingent on the presence of marine reserves, or the type of algal resource available.

## Materials and methods

### STUDY SEASCAPE

Moreton Bay is a large subtropical embayment on the south-east coast of Queensland, Australia. It comprises a heterogeneous seascape that includes coral reefs, mangrove forests and several reserves that are closed to fishing. Herbivorous fish are harvested in a commercial net fishery that targets rabbitfish (*Siganus fuscescens*) and by spearfishers targeting parrotfish (Scaridae) and surgeonfish (Acanthuridae), particularly bluebarred parrotfish (*Scarus ghobban*) and Australian sawtail (*Prionurus microlepidotus*) (Tibbetts & Townsend 2010; Olds *et al.* 2012a). We quantified the joint effect of connectivity and reserves on herbivory rates and the composition of herbivorous fish assemblages at 15 locations in Moreton Bay: seven were protected in no-take marine reserves and eight were on reefs open to fishing (Fig. 1).

The degree of connectivity between mangroves and reefs was measured from benthic habitat maps using ArcGIS (ESRI) (source: Healthy Waterways). We based connectivity measurements on the distance of reefs from mangroves and we sampled reefs that were near to ( $n = 7$ ) and far from ( $n = 8$ ) mangroves.



**Fig. 1.** Marine reserves, coral reef and mangrove habitats of central Moreton Bay, Australia. Survey locations depicted as circles over coral reef habitat.

We classified reefs as ‘near’ if they were within 250 m of the edge of mangroves, whereas reefs that were at least 500 m from mangroves were classified as ‘far’ (refer Olds *et al.* 2012a). This classification is based on the mobility of fish species in these types of seascapes (Boström *et al.* 2011; Wedding *et al.* 2011; Pittman & Olds 2015). Thus, in this case, habitats classified as near to mangroves were within the daily home ranges of adult herbivorous fish species that are common in the study area (i.e. parrotfish, rabbitfish and surgeonfish) (Davis *et al.* 2014; Green *et al.* 2015; Olds *et al.* 2014b), whereas classified as far from mangroves were not.

#### HERBIVORY EXPERIMENTS

We quantified spatial variation in herbivory (i.e. rate of algal removal), focusing on two types of herbivorous fish: grazers (e.g. parrotfish and surgeonfish) and browsers (e.g. rabbitfish). The principal technique was to place known quantities of algae to the environment and to monitor their fate over time. Low-profile turf algae were deployed to measure grazing whereas fleshy macroalgae, *Sargassum flavicans*, were deployed to measure browsing. These algae were selected due to their importance as major food items for numerous species of fish in Moreton Bay (Olds *et al.* 2014a), and their previous use in similar experiments conducted elsewhere (Hoey & Bellwood 2010a; Marshall & Mumby 2012).

Rates of herbivory were measured by deploying ten preconditioned terracotta tiles (11 × 11 × 1 cm, each supporting an extensive coverage of turf algae) and ten haphazardly selected macroalgal thalli at each of the 15 locations selected. Before the

experiment, tiles were left inside fish exclusion cages at a single reef for 6 weeks to grow a dense coverage of turf algae. During the experiment, nine experimental units (for both tiles and thalli) were available (not caged) to herbivorous fish for consumption, whilst one unit per location was inside a fish exclusion cage (0.7 × 0.7 × 0.7 m fitted with 10-mm monofilament mesh); this served as a procedural control for changes in algal cover and biomass not attributable to fish grazing. Turf grazing was quantified as the reduction in algal cover over 6 days of deployment (following Albert, Udy & Tibbetts 2008; Smith, Hunter & Smith 2010; Marshall & Mumby 2012). Macroalgal browsing was quantified as the reduction in algal weight over the same period (following Hoey & Bellwood 2010a; Vergés *et al.* 2011; Michael *et al.* 2013). Deployments were long enough to measure reductions due to fish consumption (based on visual observations), but short enough to avoid complete resource depletion. The long deployments resulted from low rates of herbivory in the study area (when compared to tropical studies) and precluded meaningful videography of algae consumption. Rates of algal removal were an order of magnitude greater outside of exclusion cages (see Appendix S1, Supporting information).

#### FISH SURVEYS

The species composition and abundance of fish assemblages were assessed with underwater visual census (UVC). Five replicate 50 × 4 m UVC belt transects were surveyed at each location within 2 h of low tide (when mangroves were dry and not accessible to fish) so that fish were concentrated on subtidal reefs (Olds *et al.* 2013). Replicate transects were positioned parallel to the reef slope (at depths of 1–3 m below the lowest astronomical tide) and separated by a minimum of 50 m. The same diver surveyed all transects, identified herbivorous fish to species level and recorded the abundance and size of all fish >5 cm total length (TL). The accuracy of size estimates was evaluated using the standard fish model method (Olds *et al.* 2014b). Fish density and size estimates were then converted to biomass using published length–weight relationships (Kulbicki, Guillemot & Amand 2005). Herbivorous fish species were classified as grazers or browsers according to their feeding behaviour (Hoey & Bellwood 2010a; Olds *et al.* 2012a; Edwards *et al.* 2014).

#### DATA ANALYSIS

The influence of reserves and mangrove–reef connectivity (both fixed factors) on herbivory and herbivore biomass was examined using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). To quantify the potential impact of water quality on herbivores and herbivory, we included an index of water quality (representing spatial variation in total nitrogen, turbidity and salinity) in analyses as a covariate (following Olds *et al.* 2014a). Water quality data were obtained from the local Ecosystem Health Monitoring Program (EHMP 2015) (see Appendix S2). Water quality did not, however, influence the interaction between reserve and connectivity effects (Appendix S2) and so was not included in the final model. Separate analyses were then conducted to examine reserve and mangrove–reef connectivity effects on grazing (i.e. turf algae removal) and browsing (i.e. macroalgae removal) herbivory (expressed as the average removed per day over 6 days of deployment). Analyses were based on modified Gower (Log<sub>2</sub>) similarity measures (which

emphasize differences in the magnitude of variables, such as algal biomass or cover, over differences in composition; Anderson *et al.* 2011).

Canonical analysis of principal coordinates (CAP) was used to visualize significant factors identified by PERMANOVA and to identify fish species that were correlated with significant factors (Anderson & Willis 2003). Similarity percentage contribution (SIMPER) analyses were then used to identify which species of herbivorous fish were primarily responsible for differences between levels of significant factors.

Distance-based linear models (DistLM; McArdle & Anderson 2001) were used to quantify how herbivory related to the biomass of different herbivorous fish species. Analyses were conducted separately for grazing (i.e. turf algae removal) and browsing (i.e. macroalgae removal), and examined relationships with the biomass of (i) herbivore functional groups (i.e. browsers, grazers and territorial herbivores); (ii) herbivore families; and (iii) individual herbivore species. Fish data were first tested for collinearity, and data for each fish species were transformed where necessary. Models were fitted using forward stepwise selection, and the strongest model was chosen using a corrected Akaike's information criterion (AICc).

## Results

### RESERVE AND CONNECTIVITY EFFECTS ON HERBIVORY

Grazing of turf algae was significantly greater on protected than on fished reefs, irrespective of whether either reef type was close or far from mangroves (Table 1; Fig. 2). By contrast, browsing of macroalgae was influenced by both conservation status and mangrove–reef connectivity (Table 1; Fig. 2). Macroalgal removal was greater on fished than on protected reefs that were far (>500 m) from mangroves, but did not differ between protected and fished reefs that were near to mangroves (Table 1; Fig. 2).

### RESERVE AND CONNECTIVITY EFFECTS ON HERBIVORES

The conservation status of reefs was associated with significant spatial variation in the species composition of herbivorous fishes (Table 1; Fig. 3). The biomass of *Acanthurus dussumieri* (pencil surgeonfish), *S. fuscescens* (black rabbitfish) and *P. microlepidotus* (Australian

sawtail) was greatest on protected reefs (Fig. 3). By contrast, the biomass of *Abudefduf bengalensis* (Bengal sergeant) was greatest on fished reefs (Fig. 3). Mangrove–reef connectivity did not influence assemblage composition (Table 1).

### FISH SPECIES THAT STRUCTURE HERBIVORY

Few herbivorous fish species appear to structure spatial variation in rates of herbivory (Table 2). The biomass of two species of surgeonfish (i.e. pencil surgeonfish and Australian sawtail) was correlated with spatial variation in grazing herbivory (i.e. turf algae removal). The spatial distribution of pencil surgeonfish biomass on reefs was linked to 26% of the total variation in removal of turf algae (Table 3). The spatial distribution of Australian

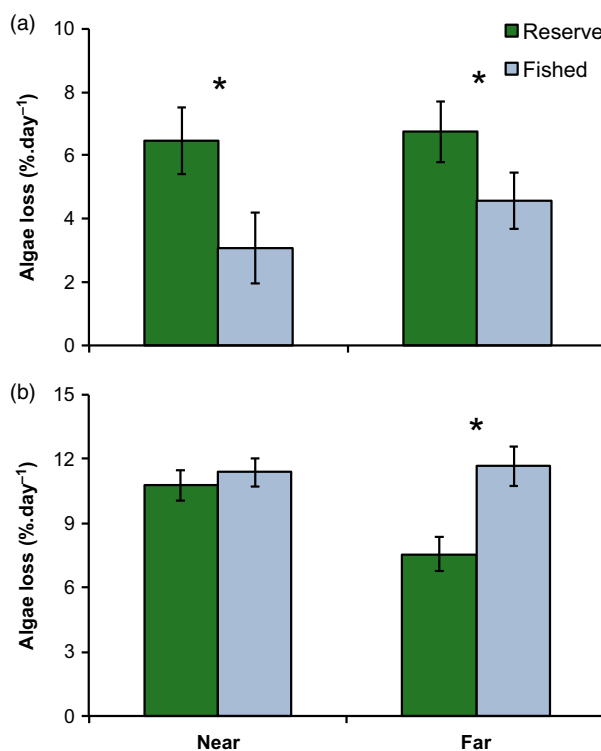


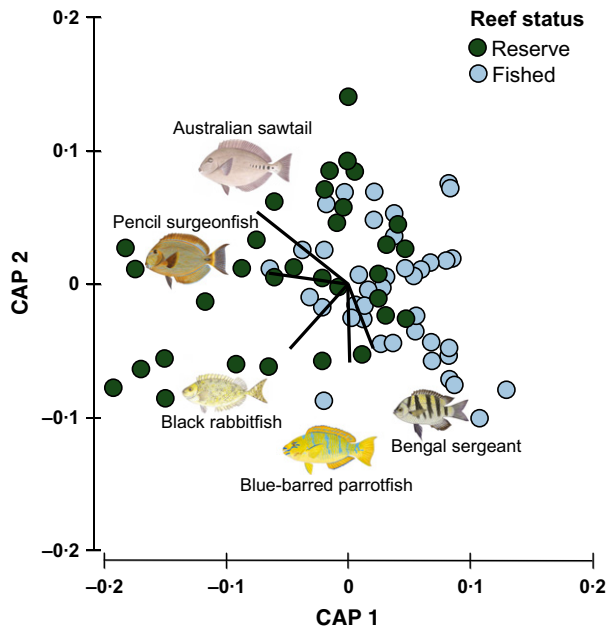
Fig. 2. Rate of algal loss (mean  $\pm$  SE) for turf algae (a) and macroalgae (b) on reserve and fished reefs near to (<250 m) and far from (>500 m) mangroves. \*Significant differences between reserve and fished reefs (identified by pairwise *post hoc* analyses).

**Table 1.** Summary of permutational multivariate analysis of variance (PERMANOVA) examining spatial variation in herbivory (i.e. grazing and browsing rates) and the composition of herbivorous fish assemblages

Source of variation	d.f.	Grazing rates		Browsing rates		Herbivorous fish	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Conservation status (C)	1	10.18	<b>0.001</b>	7.11	<b>0.006</b>	2.46	<b>0.018</b>
Mangrove–reef connectivity (M)	1	0.71	0.408	4.75	<b>0.030</b>	1.53	0.142
C $\times$ M	1	2.09	0.147	6.37	<b>0.012</b>	0.51	0.828

Values in bold are significant at  $P < 0.05$ .

sawtail biomass contributed an additional 22% to the variation linked to pencil surgeonfish (Table 3). The cumulative contribution of these two surgeonfish species



**Fig. 3.** Constrained canonical analysis of principal coordinates (CAP) displaying spatial relationships among herbivorous fish assemblages on marine reserve and fished reefs and species correlations with canonical axes (e.g. pencil surgeonfish were positively correlated with reserve reefs and Bengal sergeant were positively correlated with fished reefs). Fish illustrations sourced from [www.efishalbum.com](http://www.efishalbum.com).

accounted for approximately half of the total variation in turf algae removed. By contrast, the biomass of no herbivorous fish species, family or functional group was significantly correlated with spatial variation in browsing herbivory (i.e. macroalgae removal) (Table 3).

## Discussion

Both connectivity and reserve protection shaped herbivory on coral reefs. Protected reefs supported a greater biomass of herbivorous fishes, which led to increased grazing of turf algae on reefs; this reserve effect was independent of proximity to mangroves. Proximity to mangroves did, by contrast, matter for the consumption of macroalgae on reefs: browsing was significantly lower on protected reefs far from mangroves. Our results on herbivory in the context of habitat linkages and conservation strongly suggest that landscape connectivity and reserve protection can jointly affect ecological functions in ecosystems. Few studies have directly quantified the influence of landscape features on ecological functions (Pages *et al.* 2014), and this is rarely considered in a conservation context (*sensu* Cumming 2011; Olds *et al.* 2015).

Ecosystems that are protected in nature reserves can function differently to those that are open for harvesting, both on land and in the sea (Beschta & Ripple 2009; Babcock *et al.* 2010). On coral reefs, marine reserves can enhance the biomass of exploited herbivorous fish species, which reduce macroalgal cover and increase coral recruitment on protected reefs (Mumby & Harborne 2010; Humphries, McClanahan & McQuaid 2014). In this

**Table 2.** Common herbivorous fish species recorded at coral reef locations in Moreton Bay. Species are ordered by their contribution to community-wide differences in assemblage composition between protected and fished reefs based on SIMPER (similarity percentage) analysis

Herbivorous fish species	Family	Functional group	Biomass (kg 100 m <sup>-2</sup> )		SIMPER dissimilarity	
			Reserve	Fished	Contrib.%	Cum.%
Pencil surgeonfish ( <i>Acanthurus dussumieri</i> )	Acanthuridae	Grazer	2.45	0.83	31	31
Black rabbitfish ( <i>Siganus fuscescens</i> )	Siganidae	Browser	0.65	0.36	21	52
Australian sawtail ( <i>Prionurus microlepidotus</i> )	Acanthuridae	Grazer	1.02	0.26	17	69
Blue-barred parrotfish ( <i>Scarus ghobban</i> )	Scaridae	Grazer	0.55	0.41	16	85
Bengal sergeant ( <i>Abudefduf bengalensis</i> )	Pomacentridae	Omnivore	0.07	0.10	5	90

**Table 3.** Results of distance-based linear models (DISTLM) relating: (a) grazing of turf algae and (b) macroalgae browsing with the biomass of fishes. Models based on stepwise selection and evaluated using Akaike's information criterion (AICc)

Herbivory	Species	Pseudo- <i>F</i>	<i>P</i>	Proportion of variance explained
(a) Turf grazing	Pencil surgeonfish	4.64	<b>0.026</b>	0.263
	Australian sawtail	5.23	<b>0.049</b>	0.224
(b) Macroalgae browsing	Bengal sergeant	2.71	0.125	0.173

Values in bold are significant at  $P < 0.05$ .

study, the consumption of turf algae by fish was significantly enhanced on protected reefs. This positive effect of reserves on grazing was correlated with higher biomass of two species of surgeonfish (i.e. pencil surgeonfish and Australian sawtail). Both species are harvested by spearfishers in the study area (Tibbetts & Townsend 2010; Olds *et al.* 2012a). These species can consume both turf and macroalgae and regularly graze on turf algae in the study area (Olds *et al.* 2012a; Gilby 2015), but their dietary ecology has not been well studied (Choat *et al.* 2006; Downie *et al.* 2013; Basford *et al.* 2015). Neither species is known to utilize mangroves (Olds *et al.* 2013; Igulu *et al.* 2014), which may explain the absence of any significant proximity effect between reefs and mangroves. We contend that turf grazing by surgeonfish may be important for the functioning of coral reefs in Moreton Bay and suggest that these fish should be priority targets for further research and conservation. Indeed, turf grazing by these species may have provided the mechanism that enabled reefs that were protected in reserves to resist the impact of extreme floods that struck the region in 2011 (Olds *et al.* 2014a).

The combined influence of connectivity and reserves on rates of browsing on macroalgae supports the contention that landscape context can structure the functional effects of protected areas (Bengtsson *et al.* 2003; Cumming 2011; Nagelkerken *et al.* 2015), but the precise nature of this effect ran counter to our expectations. Macroalgal browsing was lower on isolated protected reefs than on all fished reefs, or protected reefs near mangroves. This joint effect of connectivity and marine reserves on browsing was not correlated with the biomass of any fish species. There was a weak, non-significant association with the distribution of *A. bengalensis* (Bengal sergeant), a territorial damselfish that feeds on benthic algae and invertebrates (Westneat & Resing 1988). On tropical reefs, territorial damselfish (like Bengal sergeants) impact the distribution of macroalgae: through direct consumption; by actively removing plants from their territories to cultivate preferred algae species; and by aggressively excluding other herbivores from their territories, affording certain macroalgae refuge from herbivory (Hoey & Bellwood 2010b; Ceccarelli, Jones & McCook 2011). Similar functional effects from Bengal sergeants in Moreton Bay would contribute to the spatially uneven patterns of macroalgal removal that we report. The function of browsing, however, can also be strongly influenced by the cover of macroalgae on coral reefs, with lower rates of browsing typically being reported from reefs that support a higher coverage of macroalgae (Hoey & Bellwood 2011; Chong-Seng *et al.* 2014). In Moreton Bay, macroalgae is strongly correlated with water quality and coverage is greatest on reefs in the western Bay where nutrient concentrations are highest (Gilby *et al.* 2015). Macroalgae can also be abundant on reefs that are open to fishing, and this reserve effect is independent of the proximity of reefs to mangroves (Olds *et al.* 2014a). Therefore, varia-

tion in algae cover cannot explain the spatial patterns of macroalgal browsing that we report for reefs in Moreton Bay.

Coral reefs in the subtropical waters of Moreton Bay support few herbivorous fish species, with herbivore diversity being far lower than reefs in tropical waters. Limited diversity and possibly also low functional redundancy (i.e. few species that perform similar ecological functions) may be a common feature of herbivorous reef fish assemblages on subtropical reefs, which are dominated by species that browse on macroalgae (Hoey, Pratchett & Cvitanovic 2011; Vergés *et al.* 2014). Two herbivorous reef fishes, *S. fuscescens* (black rabbitfish) and *S. ghobban* (bluebarred parrotfish), have been postulated to be important grazing and browsing herbivores in the study area (Olds *et al.* 2012a), but did not appear to influence rates of herbivory in this study. Bluebarred parrotfish are generalist herbivores that consume turf algae, macroalgae and coral tissue (Plass-Johnson, McQuaid & Hill 2013), whereas black rabbitfish are browsing herbivores with a preference for red and brown macroalgae (Pillans, Franklin & Tibbetts 2004). Both species make tidal migrations from reefs to feed in adjacent mangroves and seagrass (Mellin, Kulbicki & Ponton 2007; Olds *et al.* 2012b; Davis *et al.* 2014). Rather than feeding on the algae deployed in this study, these fish may have been consuming different algae on reefs or food items in adjacent habitats. It is, however, difficult to quantify the functional role of different herbivore species when we lack basic information on the diet, feeding ecology and movement behaviour of most herbivorous reef fish (*sensu* Brandl & Bellwood 2014). Nevertheless, our findings highlight low herbivorous fish diversity on subtropical coral reefs and suggest that ecological functions do not always scale as expected with the perceived niches or relative abundance of particular species.

Overall, our results show that both landscape connectivity and reserves can shape the functioning of ecosystems and also indicate that these effects can vary with the type of resource examined. For example, turf herbivory was greater in reserves, which may help protected reefs resist being overgrown by algae following disturbance. By contrast, greater herbivory on macroalgae on isolated fished reefs may promote reef recovery from perturbation. This finding is of fundamental significance for the conservation of all ecosystems because it means that the changes in key ecological functions associated with reserves may vary markedly depending on the landscape context in which reserves are situated.

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## Data accessibility

Data for this paper are archived in the University of the Sunshine Coast Research Bank (<http://dx.doi.org/10.4227/39/560c67c425b87>).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Effect of herbivore exclusion on algal removal.

**Appendix S2.** Influence of water quality on reserve and connectivity effects.