

Synergistic effects of reserves and connectivity on ecological resilience

Andrew D. Olds*, Kylie A. Pitt, Paul S. Maxwell and Rod M. Connolly

Australian Rivers Institute – Coast and Estuaries and School of Environment, Griffith University, Gold Coast, Qld, 4222, Australia

Summary

1. In light of the global extent and cascading effect of our impact on the environment, we design and manage reserves to restore biodiversity and the functioning of ecosystems. Mobile organisms link important processes across ecosystems, however, their roles in providing these services are often overlooked and we need to know how they influence ecosystem functions in reserves. Herbivorous fish play a key role in coral reef seascapes. By removing algae, they promote coral growth and recruitment, and help to increase resilience.

2. We examined how connectivity with mangroves affected herbivore populations and benthic succession on reefs in eastern Australia. We surveyed fish assemblages, examined reef composition and characterised benthic recruitment on reefs at multiple levels of connectivity with mangroves, in a no-take reserve and areas open to fishing.

3. Our results show that connectivity enhanced herbivore biomass and richness in reserves, and that these connectivity and reserve effects interacted to promote herbivory on protected reefs near mangroves.

4. Connectivity and reserve protection combined to double the biomass of roving herbivorous fish on protected reefs near mangroves. The increase in grazing intensity drove a trophic cascade that reduced algal cover and enhanced coral recruitment and reef resilience.

5. *Synthesis and applications.* Our findings demonstrate that ecosystem resilience can be improved by managing both reefs and adjacent habitats together as functional seascape units. By understanding how landscapes influence resilience, and explicitly incorporating these effects into conservation decision-making, we may have greater success with environmental restoration and preservation actions.

Key-words: Australia, coral reef, fish, herbivory, landscape ecology, mangroves, marine reserve, trophic cascade

Introduction

Conservation and restoration activities are focussed on the maintenance or creation of resilient, functioning ecosystems (Cadotte, Carscadden & Mirotnick 2011). Mobile organisms enhance ecological resilience by linking ecosystem functions across landscapes (Nyström & Folke 2001; Lundberg & Moberg 2003). These species connect ecological processes (e.g. Mumby & Hastings 2008) and food webs (e.g. Polis, Anderson & Holt 1997) through space. Until recently, however, their role in providing these ecosystem services has received little consideration (Massol *et al.* 2011). Spatial ecology and ecosystem

functioning are now integrated into conservation through ecosystem-based management (e.g. Foley *et al.* 2010), which is focussed on the protection of multiple species, ecosystem processes and values, and may improve our ability to manage processes across whole ecosystems (Massol *et al.* 2011). Several recent studies have explored incorporating connectivity into conservation planning (e.g. Beger *et al.* 2010; Edwards *et al.* 2010), but to better inform decision-making, we now require evaluation of its effects on ecosystem functioning in reserves.

The movement of organisms and materials across landscapes is commonly called connectivity and is important for maintaining ecological processes. Broadly speaking, connectivity is a function of habitat area, quality and arrangement, and the dispersal capabilities of individual species (Hodgson *et al.* 2009). We define habitat as units

*Correspondence author. E-mail: a.olds@griffith.edu.au

of biophysical structure and focus on the potential of habitat connectivity, the connection of habitat patches by migrating organisms (Lindenmayer & Fischer 2007), to influence ecological processes across landscapes. Habitat connections are pervasive in ecology and help sustain biodiversity and ecosystem functions (Staddon *et al.* 2010). Their influences on the spatial distribution of ecological processes (e.g. herbivory, predation, pollination and seed dispersal) are effected through: large mammal migrations in terrestrial landscapes (e.g. Thaker *et al.* 2011); bird movements in agricultural and natural ecosystems (e.g. Garcia, Zamora & Amico 2010); marine subsidies to island food webs (e.g. Spiller *et al.* 2010); and fish passage among reef seascaapes (e.g. Grober-Dunsmore *et al.* 2009). In light of the extent and cascading effects of our impacts on global ecosystems (Estes *et al.* 2011), we manage reserves to restore ecosystem functioning and have recorded cascading effects of protection on ecological processes (e.g. Kauffman, Brodie & Jules 2010), succession and resilience (e.g. Mumby & Harborne 2010). It has been suggested, however, that resilience theory must be integrated into the framework of landscape ecology, culminating in the concept of spatial resilience, which focuses on the importance of location, connectivity and context for ecosystem resilience (Nyström & Folke 2001; Cumming 2011). This has important implications for management that seeks to promote connectivity and enhance resilience, yet, we know little about how connectivity affects ecosystem functions in reserves (McCook *et al.* 2009).

The effects of habitat connectivity on ecosystem functioning in reserves may be easiest to discern in coral reef seascaapes, where the spatial context of habitats can affect grazing dynamics (e.g. Madin, Madin & Booth 2011), predator–prey interactions (e.g. Dorenbosch *et al.* 2009) and food webs (e.g. Heck *et al.* 2008). Thus, well-connected reef seascaapes may behave differently to those that are isolated (*sensu* Nyström & Folke 2001). Herbivorous fish play a critical role on reefs by removing algae, which promotes coral growth and recruitment and helps maintain coral dominance. In doing so, herbivores sustain resilience by enhancing the capacity of reefs to absorb perturbations and regenerate without slowly degrading or changing state (Hughes *et al.* 2010). Numerous studies have demonstrated the importance of herbivorous fish in structuring reef succession (e.g. Hixon & Brostoff 1996; Burkepile & Hay 2010) and in preventing and reversing shifts to macroalgae dominance (e.g. Done 1992; Hughes *et al.* 2007). Most studies have, however, been conducted at small scales (i.e. 10–100 s of metres) (but see Bellwood, Hoey & Hughes 2012), and research on the influence of spatial ecology is lacking.

Mangroves can be important nurseries and foraging areas for herbivorous reef fish (e.g. Mumby *et al.* 2004; Olds *et al.* 2012a), and connectivity with mangroves can increase grazing on reefs nearby (Mumby & Hastings 2008). Exploited herbivore populations can also recover on protected reefs where they may subsequently reduce

algal cover and enhance coral recruitment (e.g. Mumby *et al.* 2007). It is logical, therefore, to expect that connectivity and reserve effects may operate synergistically to enhance resilience on protected reefs near mangroves (*sensu* Nyström & Folke 2001; Cumming 2011). It is uncommon, however, for the design of reserve networks to explicitly consider connectivity between habitats (Steneck *et al.* 2009), and we lack any evaluations of whether habitat connectivity can promote ecosystem functioning in reserves.

We examined the influence of habitat connectivity and protection on herbivore and benthic assemblages in Moreton Bay Marine Park (MBMP), eastern Australia. In MBMP, roving herbivores are more abundant on protected reefs near mangroves than on protected isolated reefs, or reefs open to fishing (Olds *et al.* 2012a). We determined that herbivore biomass and richness was also greater on protected reefs close to mangroves and established the following hypotheses: (i) benthic succession on artificial substrates accessed by herbivores (as a proxy for grazing) will correlate with patterns in herbivore biomass and richness (i.e. herbivores will reduce macroalgae and turfalgae establishment and promote the settlement of coralline algae and coral) and (ii) cascading effects from herbivores will reduce algal cover and enhance coral recruitment on protected reefs near mangroves. We demonstrate that connectivity can enhance the biomass and richness of herbivores in reserves and exert cascading effects that alter benthic reef succession, which may improve the resilience of protected reefs near mangroves.

Materials and methods

SEASCAPE ANALYSIS

Moreton Bay is a subtropical embayment south of the Great Barrier Reef. It supports a heterogeneous seascape containing fringing reefs downshore of adjacent mangroves (Olds *et al.* 2012b). We quantified the composition of herbivorous fish assemblages, water quality and benthic succession at five reef locations in Moreton Bay (Fig. 1). Surveys and experiments were conducted between November 2009 and January 2011. Only one effective no-take reserve protected these habitats at the time of our study, and we compared fish assemblages and benthic succession between this reserve (protected since 1997) and four unprotected control locations. At each location, we examined one reef close (< 250 m) to mangroves and one distant (> 500 m) from mangroves. Distances were scaled to the daily home ranges of common species in coastal Queensland, and connectivity was quantified as habitat isolation from existing habitat maps for Moreton Bay (source: Queensland Department Environment and Resource Management) using ArcGIS (ESRI, Redlands, CA, USA) (refer Olds *et al.* 2012b). Studies of spatial patterns in ecology can only infer causality after testing and falsifying potential alternative explanations (Mumby *et al.* 2004), and we verified that fish distributions were not explained by covariation of mangrove area, inundation or composition with isolation (Olds *et al.* 2012a).

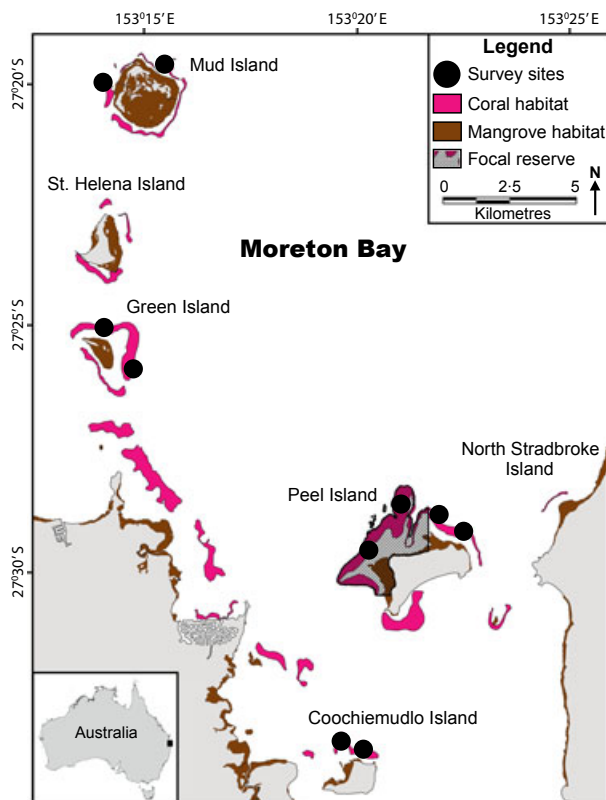


Fig. 1. Mangroves and coral reefs of central Moreton Bay, Australia. Black circles depict survey sites.

HERBIVOROUS FISH

Herbivorous reef fish were surveyed using underwater visual census conducted at low tide (when nearby mangroves were dry and not accessible) along five replicate 50×4 m transects. Individual fish were identified to species and placed into 5-cm size categories. Fish densities (taken from Olds *et al.* 2012a) and size estimates were converted to biomass using published length–weight relationships (following Albert, Udy & Tibbetts 2008). The richness of herbivorous fish species was calculated as a surrogate for functional diversity (Micheli & Halpern 2005). This approach has some drawbacks, but is recommended when the functional traits of species that correlate with ecosystem functioning are not known, or are difficult to measure (Cadotte, Carscadden & Mirochnick 2011). Fish were organised into the following, non-exclusive, groups: harvested herbivores, roving herbivores, territorial herbivores and individual species. Herbivorous fish are harvested locally in a commercial fishery targeting black rabbitfish *Siganus fuscescens* Houttuyn and by spearfishers targeting parrotfish (Scaridae) and surgeonfish (Acanthuridae), particularly bluebarred parrotfish *Scarus ghobban* Forskål and Australian sawtail *Prionurus microlepidotus* Lacepède (Tibbetts & Townsend 2010; Olds *et al.* 2012a). Different herbivore functional groups have contrasting effects on algal assemblages, which contribute to variable succession following disturbance (Burkepile & Hay 2010). We calculated the density of roving herbivorous fish from the Acanthuridae, Ephippidae, Kyphosidae, Pomacentridae, Scaridae and Siganidae (following Hoey, Pratchett & Cvitanovic 2011) and the density of territorial damselfish (Pomacentridae) (Ceccarelli, Jones & McCook 2011). Roving herbivores affect succession by consuming algal biomass, whereas territorial

damselfish exclude other herbivores from their territories and facilitate the establishment of different algal assemblages (see Hixon & Brostoff 1996; Ceccarelli, Jones & McCook 2011). Roving herbivores were categorised as browsers or grazers (see Appendix S1 in Supporting Information). Browsers consume fleshy macroalgae and can potentially reverse phase shifts from coral to macroalgal dominance, whereas grazers feed on lower profile algae (e.g. turfalgae) and may be important in preventing phase shifts (Hughes *et al.* 2007).

BENTHIC ASSEMBLAGES, SUCCESSION AND HERBIVORE EXCLUSION

To test the effects of herbivore exclusion on benthic succession, we deployed roughened flat PVC tiles (total surface area 150 cm^2) in August 2010. PVC was chosen because it is inert, supports biotic assemblages similar to natural substrata and provides a consistent surface across treatments. (refer Smith, Hunter & Smith 2010). Twelve tiles were deployed at each site, attached to concrete blocks (following Albert, Udy & Tibbetts 2008), positioned parallel to the substrate $c.1$ m below lowest astronomical tide and raised with 1-cm spacers to allow coral settlement on undersides (following Mundy 2000). To simulate loss of macrograzers, half of the artificial substrates at each site were caged. Exclusion cages were constructed from an aluminium frame ($0.7 \times 0.7 \times 0.7$ m) covered with monofilament mesh (10 mm diameter). Cages were cleaned every 2 weeks to prevent fouling. Cage controls were not included in the experiment because previous experiments have shown negligible effects of caging on light and water motion where cages are cleaned frequently (e.g. Hixon & Brostoff 1996; Diaz-Pulido & McCook 2003; Albert, Udy & Tibbetts 2008). To evaluate potential cage effects, we logged light over 3 days and quantified water motion inside and outside cages using Odyssey Data Recorders (Dataflow Systems, Christchurch, New Zealand) and clod cards (following Albert, Udy & Tibbetts 2008).

Benthic assemblages were examined monthly from September to December 2010. To monitor succession, the upper surface of tiles was photographed underwater and the primary coverage of encrusting biota was determined from digital images using Coral Point Count (National Coral Reef Institute, Dania Beach, FL, USA). A grid of 25 points was randomly overlaid on each image, and the substrate underlying each point was classified as bare tile, turfalgae, macroalgae, crustose coralline algae (CCA), non-coraline algal crusts, articulated algae, stony coral, soft coral, sponge, bryozoan or polychaete worms (following Albert, Udy & Tibbetts 2008; Smith, Hunter & Smith 2010). Tiles were removed in January 2011 and recruitment of stony corals was quantified. We had intended to continue the experiment throughout summer, but it was truncated by extreme flooding of the Brisbane River, which discharged a riverine plume into Moreton Bay. Tiles were collected immediately after the flood peak, but little sediment had been deposited and recruits retained intact skeletons. After retrieval, tiles were bleached overnight in a 10% NaOH solution to remove algae and soft organisms and reveal coral skeletons. Tiles were examined under a stereomicroscope, and recruits on the upper, lower and vertical sides were counted and identified (following Babcock *et al.* 2003).

To investigate the influence of herbivores on natural reef substrata, benthic assemblages were surveyed along the same belt transects used to examine fish biomass, and the cover of

turfalgae, macroalgae, CCA, stony coral, soft coral and sponge was quantified (see Olds *et al.* 2012a).

WATER QUALITY

To check whether herbivores and benthic reef assemblages were also responding to co-variation in water quality, we quantified nutrient concentrations (i.e. total nitrogen and phosphorus, and dissolved ammonium, nitrogen oxides (nitrite and nitrate) and inorganic phosphorus) from samples taken at each site. Samples were collected on three occasions (in August, October and December 2010) from just above the coral on ebb tides (to capture water from both the reef and adjacent intertidal mangroves) using sterile 50-mL syringes. Total and dissolved (filtered through 0.45- μm polyethersulfone membrane filters) nutrient samples were stored frozen in rinsed polyethylene containers and analysed using an automated LCHAT 8000QC flow injection analyser.

DATA ANALYSIS

Reserve and connectivity effects on fish and cascading effects to benthic organisms were evaluated using a modified Control–Impact design. Interactions between protection and connectivity were analysed by comparing the reserve to the average of four control locations using asymmetrical analysis of variance (Underwood 1992). The method for constructing an asymmetrical ANOVA involves combining the sum of squares values from separate ANOVAs to examine whether the single reserve location differs from the average of the controls (see Olds *et al.* 2012a). Two-factor ANOVAs were conducted for herbivore and natural substrate variables, and three-factor ANOVAs were conducted for encrusting groups on tiles. The factors were as follows: connectivity (a fixed orthogonal factor), location (a random orthogonal factor) and exclusion (a fixed orthogonal factor used only in tile analyses). Cochran's C tests were used to test homogeneity of variance, and data were $\ln(x + 1)$ transformed where necessary to reduce heterogeneity. If transformation failed to stabilize variances, raw data were analysed because ANOVA is robust to moderate violations of this assumption (Underwood 1997). Residual heterogeneity was driven by outliers and the aggregated (for roving grazers) or low and variable (for CCA, soft corals and bare surfaces on tiles and CCA on natural substrates) distribution of particular variables. When analysing heteroscedastic data, α is often reduced to 0.01 to limit Type I errors (i.e. detecting apparent reserve effects where none exist). Reducing α , however, increases potential for Type II errors (i.e. detecting no reserve effects where they actually exist) (Mapstone 1995). Therefore, we reduced α to 0.025 to limit possibility of Type I errors and minimize effects on Type II error, whilst ensuring that marginal results were interpreted cautiously (Quinn & Keough 2002). Post hoc Tukey's tests were used where appropriate to determine which of the means differed.

To investigate reserve and connectivity effects on benthic assemblage composition (natural substrates) and succession (tiles), data were examined using non-metric multidimensional scaling (nMDS) (Clarke 1993) applied to Bray–Curtis similarity matrices, calculated on square-root transformed data. Data were transformed to improve the distribution of residuals. Although the full data set was analysed, the ordination of benthic succession over time showing individual replicates was too crowded to display effectively. Consequently, the ordination of mean values for each site and sampling event (which produced the same

pattern and interpretations) is presented. Coherent groups of samples were defined using similarity profile (SIMPROF) tests ($\alpha = 0.01$, 999 permutations). SIMPROF is a permutation test for multivariate structure among samples with no a priori grouping (Clarke, Somerfield & Gorley 2008) and is appropriate for examining asymmetrical data (cf. MANOVA and ANOSIM). This group structure was superimposed over the nMDS ordination as were vectors depicting the correlation of individual taxa with the nMDS space. Vectors indicate the direction of greatest increase in cover for taxa most highly correlated with the space. Vector direction was determined by the regression of each taxon on the nMDS space, with vector length reflecting the R^2 value for each regression (e.g. Ceccarelli, Jones & McCook 2011).

BEST analyses were performed to identify herbivore biomass and water column nutrient variables that best explained patterns of similarity in the composition of tile assemblages (Clarke, Somerfield & Gorley 2008). Analyses were applied to Bray–Curtis similarity matrices, calculated on square-root transformed data. Biomass of roving and territorial herbivores and concentrations of water column nutrients were included in the explanatory data matrix. Water quality data were examined for covariation with patterns in herbivore biomass and benthic assemblage composition using asymmetrical ANOVA. The analysis design was identical to that adopted to examine fish biomass. Multivariate analyses were performed using PRIMER analytical software (PRIMER-E Ltd, Plymouth, UK).

Results

HERBIVOROUS FISH

Habitat connectivity enhanced reserve performance in promoting herbivore richness and the biomass of roving herbivorous fish on reefs (Fig. 2). Their biomass on protected reefs close to mangroves was approximately double that recorded on unprotected reefs close to mangroves and approximately four times greater than reefs distant from mangroves regardless of their protection status (Fig. 2, Appendix S2). This pattern largely reflected macroalgal browser biomass, particularly *S. fuscescens*, which was greatly enhanced on protected reefs close to mangroves (Appendix S2) and comprised 33–72% of the biomass of roving herbivores. Reserves did not influence the biomass of roving browsers on reefs far from mangroves or the biomass of territorial herbivores (Appendix S2). The biomass of roving grazers, and two other harvested herbivores, *P. microlepidotus* and *S. ghobban*, was greater on reserve reefs than on unprotected reefs (Appendix S2).

BENTHIC ASSEMBLAGES AND SUCCESSION

The enhanced richness and biomass of roving herbivores on well-connected protected reefs had a cascading effect on the composition and succession of benthic assemblages on reef tiles. Succession progressed with different trajectories on caged and uncaged tiles (Fig. 3). Succession on caged tiles was characterised by increased coverage of red and brown macroalgae, whilst on uncaged tiles, it was typified by a greater cover of turfalgae (see eigenvectors on Fig. 3). After the first two events, however, uncaged

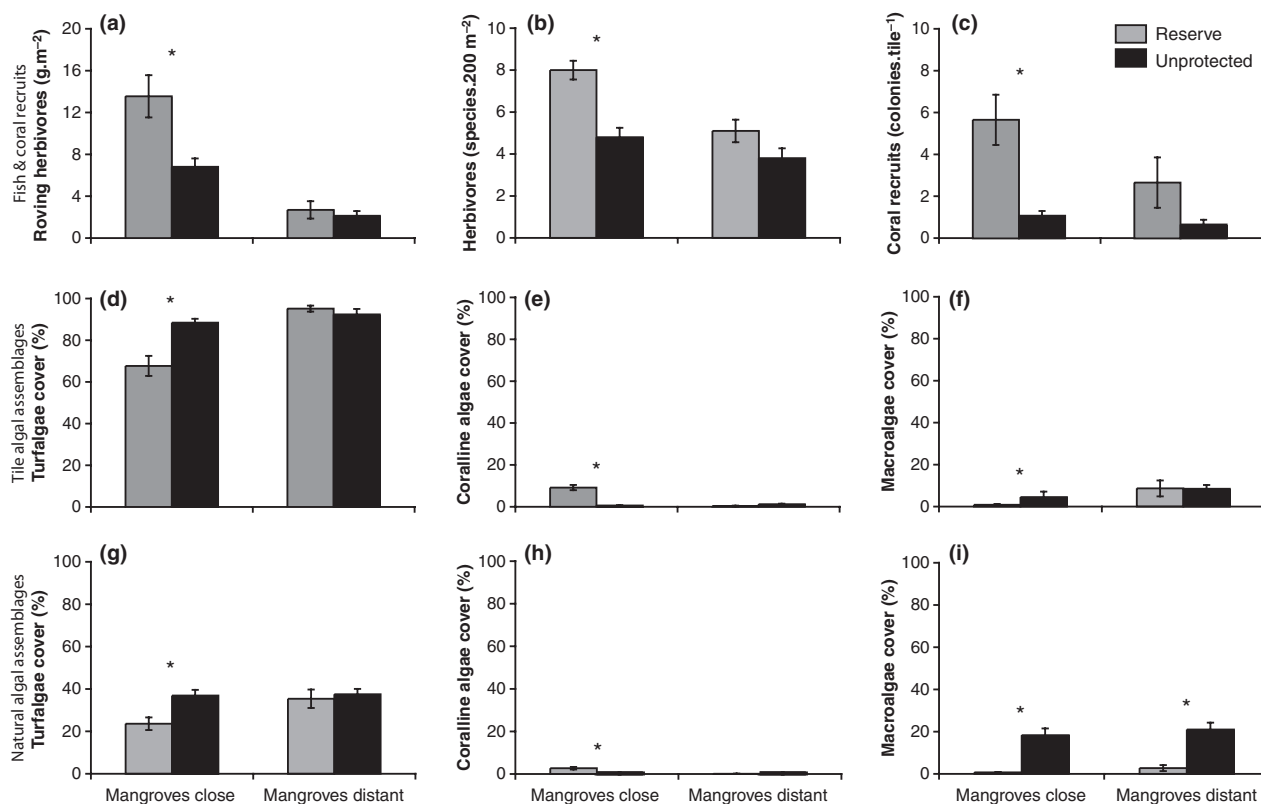


Fig. 2. Effects of reserves and connectivity on: roving herbivore biomass (a); herbivore richness (b); density of coral recruits (c); cover of turfalgae, crustose coralline algae (CCA) and macroalgae (d–f) on tiles after 4 months deployment; and cover of turfalgae, CCA and macroalgae on natural substrate (g–i) (mean \pm SE). Significant differences between reserve and unprotected locations represented by*.

tile assemblages on protected reefs close to mangroves diverged from other uncaged tiles (Fig. 3). At the completion of the experiment (December 2010), benthic assemblages on uncaged tiles on protected reefs close to mangroves differed from those on unprotected reefs, those on protected reefs far from mangroves and from those on caged tiles (SIMPROF $P = 0.01$) (Fig. 3). Uncaged tiles on protected reefs close to mangroves supported more diverse assemblages characterised by turfalgae, macroalgae, CCA and soft corals and bare areas created by grazers, whilst other uncaged tiles were dominated by turfalgae and caged tiles were typified by macroalgae and turfalgae (see eigenvectors and pie charts on Fig. 3). The cover of turf and macroalgae on uncaged tiles was lower on protected reefs close to mangroves, whilst CCA cover and the density of coral recruits were higher on these reefs (Fig. 2, Appendix S2). Reserves did not influence algae or coral cover on reefs far from mangroves. The cages used did not significantly reduce light (light intensity: ambient $485 \pm 95 \mu\text{E m}^{-2}\text{s}^{-1}$ and caged $379 \pm 81 \mu\text{E m}^{-2}\text{s}^{-1}$, $P > 0.05$) or water motion (clod card loss: ambient: $9.4 \pm 0.5 \text{ g day}^{-1}$ and caged $8.9 \pm 0.3 \text{ g day}^{-1}$, $P > 0.05$).

The cover of turfalgae on natural substrata was lower on protected reefs close to mangroves; CCA cover was also higher on these reefs, whilst macroalgae cover was lower on reserve reefs than on unprotected reefs (Fig. 2, Appendix S2).

POTENTIAL COVARIATION OF WATER QUALITY

The composition of assemblages on artificial reef tiles was best predicted by a combination of roving herbivore biomass and the concentration of nitrogen oxides (nitrite and nitrate) in the water column (R value = 0.439, $P = 0.01$). Water column nutrient concentrations, however, did not differ (i.e. $P > 0.05$) between reserve and unprotected locations supporting close or isolated reefs and mangroves (Appendix S3). The correlation of herbivore biomass and benthic assemblages with habitat connectivity and reserve protection was, therefore, not affected by co-variation in water quality.

Discussion

Overharvesting is common to marine, freshwater and terrestrial ecosystems world-wide, where losses of large consumers have had cascading effects on ecosystem processes and resilience (Estes *et al.* 2011). Trophic cascades that reverse these effects, however, are hard to detect, display variable response times, and are frequently context-dependent (Babcock *et al.* 2010; Terborgh & Estes 2010). We demonstrated a positive effect of reserves on roving grazer biomass, and synergistic effects of connectivity and protection on roving browser biomass and herbivore richness. Our results show that the interaction

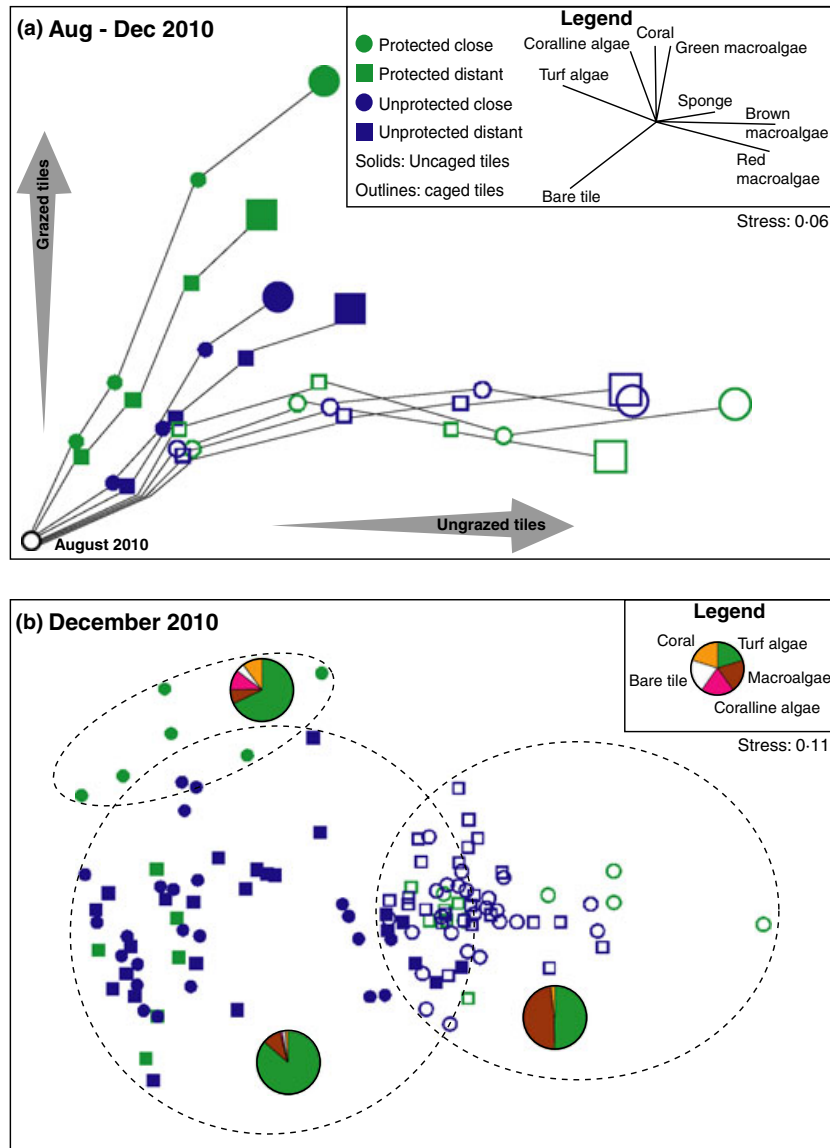


Fig. 3. Multidimensional scaling (MDS) ordination of relationships among tile assemblages on reserve and unprotected reefs at each level of connectivity. (a) Successional trajectories showing how assemblages changed over time, points represent multivariate centroids for each treatment and time. Sampling began in August 2010 (lower left of ordination) and ended in December 2010 (enlarged shapes to upper right of ordination). Eigenvectors indicate direction of greatest cover increase for taxa with strongest correlation to ordination space (length is proportional to R^2). (b) Similarity of tile assemblages in December 2010. Dashed lines delineate coherent groups defined by SIMPROF analysis ($P = 0.01$). Pie charts display composition of benthic assemblages in each group.

between reserve and connectivity effects enhanced grazing intensity on protected reefs near mangroves, which suppressed turf and macroalgae and facilitated coral recruitment. These findings support the assertion that connectivity can play an important role in mediating cascades and their effects on ecosystem functioning (e.g. van Nes & Scheffer 2005; Estes *et al.* 2011). This represents a strong case for greater integration of spatial ecology into ecosystem-based management (e.g. Foley *et al.* 2010; Massol *et al.* 2011) and suggests that by explicitly incorporating connectivity into conservation planning, we may be better placed to restore ecosystem functioning in reserves.

The critical role of herbivorous fish in removing algae, promoting coral growth and recruitment, and maintaining

reef resilience is widely recognised (Hughes *et al.* 2010). Recent studies (e.g. Mumby & Hastings 2008; Adam *et al.* 2011; Vergés *et al.* 2011) have shown that connectivity can improve reef resilience. Given the potential for reserves to further enhance herbivore biomass and reef resilience (Mumby & Harborne 2010), it is surprising that we lack evaluations of whether the effects of habitat connectivity and protection interact. This is emphasised by studies that have demonstrated the real (e.g. Olds *et al.* 2012a) and modelled (e.g. Edwards *et al.* 2010) potential for habitat connectivity to enhance herbivore biomass in reserves. We have shown empirically that mangrove connectivity can enhance herbivore biomass and richness on reefs and alter benthic composition and succession. These synergistic

effects on algal growth and coral recruitment should maintain coral dominance on reefs across a broader range of environmental conditions and thereby enhance resilience of protected reefs near mangroves. We examined inshore reefs, and a lesser role for mangrove connectivity might, therefore, be expected on reefs that lie further offshore, but it is possible that similar connections also exist over larger scales. For example, the largest parrotfish species of the Indo–Pacific (*Bolbometopon muricatum*) and Caribbean Sea (*Scarus guacamaia*) play critical roles in maintaining ecosystem processes on offshore reefs, they are both subjected to overharvesting and appear to recruit to inshore habitats (particularly mangroves and adjacent lagoons) (Bellwood & Choat 2011). The long-term survival of these species and the ecosystem functions they perform may, therefore, depend on our ability to coalesce these broader habitat connections into conservation strategies that are set at the seascape scale (sensu Nyström & Folke 2001).

Herbivore removal and eutrophication can have large effects on benthic coral reef assemblages, but their relative significance is still debated (e.g. Smith, Hunter & Smith 2010). Our results indicate that coral reef succession in Moreton Bay correlates positively with herbivore biomass (and top–down control) at the scale of individual reef seascapes and negatively with water quality (and bottom–up control) across the whole ecosystem. When compared to tropical reefs in the western Pacific, coral recruitment in Moreton Bay was low (cf. Hughes *et al.* 2002; Thompson *et al.* 2011) and algal colonisation was high (cf. Albert, Udy & Tibbetts 2008; Roff & Mumby 2012). Coral recruitment was, however, greater than that recorded on nearby subtropical reefs (cf. Harriott & Banks 1995; Banks & Harriott 1996), but lower than documented rates at higher latitudes (Harriott 1992). Coral recruitment on subtropical reefs can vary greatly from year-to-year (Harriott & Banks 1995), and it will therefore be important to examine longer term temporal variation in local recruitment. Indeed, recruitment rates in Moreton Bay, and the importance of connectivity, might logically be expected to increase with subtropical range extensions of tropical species with climate change (Lybolt *et al.* 2011). Patterns in benthic succession may reflect the low biomass and diversity of herbivorous fish in Moreton Bay (Tibbetts & Townsend 2010), which as on subtropical reefs elsewhere (e.g. Hoey, Pratchett & Cvitanovic 2011), was dominated by macroalgal browsers. The low biomass and diversity of other grazing functional groups might be expected to limit the capacity of reefs to resist phase shifts to macroalgae dominance and lower resilience (refer Bellwood, Hoey & Hughes 2012). Our findings suggest, however, that the resilience of severely degraded reefs, like those in Moreton Bay (Pandolfi *et al.* 2003), can be enhanced through seascape conservation.

The synergistic effects of reserves and connectivity on herbivores, benthic succession and coral recruitment indicate that conservation based on an understanding of

spatial ecology and ecosystem functioning may also improve the resilience of other ecosystems. Indeed, consumer-driven processes (like herbivory) provide important stabilizing mechanisms for resilience in marine, freshwater and terrestrial ecosystems (Folke *et al.* 2004). In each case, the distribution of mobile organisms, and their effect on ecosystem services and resilience, is influenced by connectivity and spatial variation in the landscape (sensu Nyström & Folke 2001; Cumming 2011). These effects have, however, been degraded by a long history of overexploitation (Folke *et al.* 2004; Estes *et al.* 2011). It seems reasonable, therefore, to expect similar synergistic effects on resilience from habitat connectivity and reserves in other systems.

Our results show that mangrove connectivity can enhance herbivore biomass and richness and coral recruitment in reserves, suggesting that resilience can be improved by managing both reefs and adjacent habitats together as functional seascape units. This is important because habitats like mangroves and seagrass are threatened more by development than climate change and can benefit greatly from improved local management (Adam *et al.* 2011). To better integrate spatial ecology into management for inshore reef seascapes, it seems logical to prioritise conservation of proximally located reefs and mangroves. Questions remain, however, over the importance of scale and the nature of the connectivity–resilience relationship. We report positive effects of connectivity and marine reserves on reef resilience at a scale corresponding to daily fish movements (i.e. 100 s metres). This is similar to scales of ontogenetic shifts from nursery habitats (i.e. mangroves, seagrass and lagoons) to reefs (i.e. 100–1000 s metres), which can also affect reserve performance (Nagelkerken, Grol & Mumby 2012) and enhance reef resilience (Mumby & Hastings 2008; Adam *et al.* 2011). However, given that ecological resilience is driven by threshold dynamics (Hughes *et al.* 2010) and that fish-mediated connectivity is affected by thresholds in habitat area and isolation (Olds *et al.* 2012b), the relationship between connectivity and resilience is unlikely to be linear. It will, therefore, be critical to better characterise this relationship to improve spatial planning decision-making. With a greater understanding of how landscapes influence spatial resilience, and by explicitly incorporating the synergistic effects of connectivity into conservation planning, we will be better placed to restore and preserve resilient, functioning ecosystems.

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Supporting Information

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

Appendix S1. Herbivorous reef fish guilds.

Appendix S2. Connectivity and reserve effects on fish and benthic assemblages.

Appendix S3. Summary of water column nutrient variables.

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