Marine reserves help coastal ecosystems cope with extreme weather

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Abstract

Natural ecosystems have experienced widespread degradation due to human activities. Consequently, enhancing resilience has become a primary objective for conservation. Nature reserves are a favored management tool, but we need clearer empirical tests of whether they can impart resilience. Catastrophic flooding in early 2011 impacted coastal ecosystems across eastern Australia. We demonstrate that marine reserves enhanced the capacity of coral reefs to withstand flood impacts. Reserve reefs resisted the impact of perturbation, whilst fished reefs did not. Changes on fished reefs were correlated with the magnitude of flood impact, whereas variation on reserve reefs was related to ecological variables. Herbivory and coral recruitment are critical ecological processes that underpin reef resilience, and were greater in reserves and further enhanced on reserve reefs near mangroves. The capacity of reserves to mitigate external disturbances and promote ecological resilience will be critical to resisting an increased frequency of climate-related disturbance.

Keywords: Australia, coral reefs, disturbance, ecological resilience, flood impacts, herbivory, marine reserves, seascape connectivity

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Introduction

Environmental conservation and restoration have typically concentrated on enhancing biodiversity and increasing productivity, but with the ever-increasing global human footprint, considerable effort is now focused on maintaining resilient, functioning ecosystems (Bengtsson *et al.*, 2003; Estes *et al.*, 2011; Silliman *et al.*, 2012). Ecological resilience is the capacity of an ecosystem to resist or recover from impact without changing structure or function, or shifting to an alternate regime (Holling, 1973; Scheffer *et al.*, 2001; Hughes *et al.*, 2010). Enhancing resilience is a clear objective for new nature reserves, and may be an added benefit in those already established, but their capacity to actually affect resilience needs assessment (Bengtsson *et al.*, 2003; Gaines *et al.*, 2010; Bernhardt & Leslie, 2013).

Progress has been hampered by inherent difficulties in assessing resilience, which result from the need for large ecosystem-scale perturbation (van Nes & Scheffer, 2007; Thrush *et al.*, 2009; Mumby *et al.*, 2013a). Research has also been hindered because the ecosystem effects of

reserves are hard to detect, display variable response times, and are frequently context dependent (Babcock *et al.*, 2010; Terborgh & Estes, 2010). Furthermore, it has been suggested that reserves may have little effect on the capacity of ecosystems to withstand global-scale disturbances (e.g., rising temperatures, ocean acidification) (Cote & Darling, 2010; Darling *et al.*, 2010; Mora & Sale, 2011), but studies thus far have had mixed results (Graham *et al.*, 2011; Micheli *et al.*, 2012; Selig *et al.*, 2012; Bates *et al.*, 2014). Their potential to affect ecological resilience is likely greatest when the scale of disturbance matches reserve size, and reserves enhance ecological processes that help mitigate the type of perturbation experienced (McCook *et al.*, 2010; Halpern *et al.*, 2013) (e.g., regional weather events). Given that changes to the global climate are increasing the frequency of extreme weather events (Coumou & Rahmstorf, 2012), the potential effect of reserves on ecological resilience to these impacts requires urgent assessment.

Coral reefs are critically important ecosystems that support a large proportion of global biodiversity and provide ecosystem services for over 450 million people (Hughes *et al.*, 2010; Pandolfi *et al.*, 2011). They have, however, been subjected to a history of degradation, exploitation and pollution and are now threatened globally by rising sea temperatures, ocean acidification

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and increasingly extreme weather events (Hoegh-Guldberg & Bruno, 2010; Graham *et al.*, 2013). Maximizing the ability of reefs to resist these escalating global threats will depend on the successful management of local-scale disturbances (Edwards *et al.*, 2011).

Herbivorous fish are critical for facilitating reef resilience to local-scale perturbation, such as floods or eutrophication, because their grazing activities reduce competition between algae and corals and help maintain coral dominance (Mumby & Steneck, 2008; Hughes *et al.*, 2010; Mumby *et al.*, 2013a). The recovery of exploited herbivores in marine reserves actively reduces the cover of algae, which can subsequently promote coral growth and enhance coral recruitment (Stockwell *et al.*, 2009; Mumby & Harborne, 2010; Rasher *et al.*, 2013). These ecological processes provide important feedback mechanisms that stabilize coral reefs and help them to resist local disturbances, like storms and floods (Edwards *et al.*, 2011; Nyström *et al.*, 2012; Graham *et al.*, 2013). They can also be enhanced by the synergistic effects of connectivity with mangroves, which provide important nurseries and feeding habitats for herbivorous reef fish (Olds *et al.*, 2012a). Mangrove connectivity increases the biomass and grazing intensity of herbivorous reef fish, which helps to promote ecological resilience on coastal reefs (Mumby & Hastings, 2008; Olds *et al.*, 2012a). However, once large stands of macroalgae become established, they can be avoided by herbivorous fish and may prevent coral recruitment, thereby limiting the capacity for reef recovery (Hoey & Bellwood, 2011; Nyström *et al.*, 2012).

The catastrophic flooding of eastern Australia in January 2011 received worldwide media attention, resulted in loss of life and property, and had the potential to devastate sensitive coastal ecosystems including the Great Barrier Reef (GBR)(Crow, 2011). We examined the capacity of marine reserves to mitigate this impact on coral reefs in Moreton Bay, a subtropical embayment south of the GBR that has been advocated as a potential refuge for tropical species threatened by climate change (Lybolt *et al.*, 2011). Moreton Bay was impacted by severe flooding from the Brisbane River, which discharged the equivalent of 20 years of average annual sediment loads into the bay in a single event and deposited a thick layer of mud over 100 km² of seafloor (Gibbes *et al.*, 2014). Coral reefs in Moreton Bay that are protected in marine reserves support abundant herbivorous fish and experience higher rates of herbivory and coral recruitment than nearby unprotected reefs where herbivorous fish are harvested by commercial and recreational fishers (Olds *et al.*, 2012a,b). These reserve effects are further elevated on reefs near adjacent mangroves (Olds *et al.*, 2012a). We hypothesized that these enhanced ecological processes might impart

reserve reefs with greater resilience, but a true test of their resilience necessitates large-scale perturbation of the ecosystem (Thrush *et al.*, 2009).

We examined whether preflood differences in key ecological processes subsequently improved the capacity of reserves to resist, or recover from, flood impacts. Historic floods had already altered the composition of coral reefs in Moreton Bay (Lybolt *et al.*, 2011), so we evaluated flood effects on reef assemblages. Multivariate species data, such as these, provide an integrated measure of abundance and diversity, which is valuable when assessing variation in community responses to perturbation (Anderson *et al.*, 2011). The health and resilience of coral reefs have often been assessed by monitoring coral cover, but this approach can only improve our knowledge of ecological resilience when monitoring is conducted over many years and is coupled with data on the ecological processes and feedbacks that underpin resilience.(Hughes *et al.*, 2010; Graham *et al.*, 2011) When perturbed, stabilizing ecological processes (like herbivory) help maintain the structure and functioning of resilient ecosystems, whereas this capacity is lost in nonresilient ecosystems which can shift abruptly to an alternate regime (Scheffer *et al.*, 2001; Hughes *et al.*, 2010; Mumby *et al.*, 2013b). Understanding this relationship between perturbation (i.e. physical impact), stabilizing feedback mechanisms (i.e. key ecological processes) and ecosystem responses (i.e. effects on assemblages) is fundamental for the assessment of ecological resilience (Thrush *et al.*, 2009; Nyström *et al.*, 2012; Hughes *et al.*, 2013). Reserve effects on reef resistance trajectories were, therefore, quantified by examining the relationship between variation in physical impact variables (i.e. water quality and sedimentation), ecological process metrics, which are viewed as indicators for algal production, herbivory and calcification (McClanahan *et al.*, 2012), and temporal changes in coral assemblages.

Materials and methods

Coral assemblages

Coral assemblages were surveyed at ten locations in Moreton Bay, over three years spanning the Brisbane River floods in early 2011. Assemblages were assessed 1 year before the flood (2010), immediately postflood (2011), and 1 year postflood (2012). Four locations were inside marine reserves; remaining locations were open to fishing. Assemblages were quantified along five replicate 50 × 4 m transects at each location and event by taking digital photographs of the benthos every 2 m along each transect from 0.5 m above the substrate. Digital images were analyzed for benthic cover using Coral Point Count (Kohler & Gill, 2006). A grid of 25 points was randomly overlaid on each 1 m² image, and the substrate underlying

each point was classified as hard coral, soft coral, macroalgae, turf algae, crustose coralline algae, sponge, rubble, or sand or soft sediment (Olds *et al.*, 2012c). Coral and algae were identified to genera.

Water quality

To determine if flood effects on coral assemblages were correlated with changes in water quality, we examined annual variation in water quality (i.e. pH, salinity, secchi depth, turbidity, total nitrogen, and total phosphorus) at each reef. Data were obtained for each location (for January, from 2002 to 2012) from the Ecosystem Health Monitoring Program (EHMP, 2010).

Herbivorous fish and coral recruitment

Herbivorous reef fish were surveyed prior to the flood along the same belt transects used to examine coral assemblages. Individual fish were identified to species, and fish densities and size estimates were converted to biomass using published length–weight relationships (see Olds *et al.*, 2012b). Different herbivore functional groups exert contrasting effects on algae, which contribute to variable succession following disturbance. Browsers consume fleshy macroalgae and can reverse coral–macroalgal phase shifts, whereas grazers feed on lower profile algae (e.g., turf) and may prevent phase shifts (Hughes *et al.*, 2007). The biomass of roving browsers and grazers was quantified for each location (Olds *et al.*, 2012a).

To quantify herbivore effects on coral recruitment, 12 settlement tiles were deployed at each of ten reef locations ($n = 120$) (Olds *et al.*, 2012a). Hard coral recruitment was quantified on six tiles collected before the flood, and six tiles collected 1 year later. Tiles were examined under a stereomicroscope and recruits on all surfaces were counted and identified (following Babcock *et al.*, 2003).

Mangrove-reef connectivity can influence reserve effects on fish and coral recruitment in Moreton Bay (Olds *et al.*, 2012a, b). Therefore, connectivity was quantified as the edge-to-edge distance between habitats from benthic habitat maps, and sampling sites were selected with two levels of habitat separation (i.e. close: <250 m, and far: >500 m), which were interspersed across Moreton Bay (Olds *et al.*, 2012a).

Data analyses

Coral data were analyzed using permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) to examine flood effects on assemblages (i.e. coral genera) from reserve and fished reefs. PERMANOVA is a nonparametric multivariate analog to ANOVA, which allows direct additive partitioning of variation for complex models, but maintains the lack of formal assumptions of other nonparametric methods. To determine which sites the flood impacted, annual variation in assemblage composition at all sites was assessed with two-way PERMANOVA. The factors were: year (fixed orthogonal factor) and site (random factor). Proximity to impact source (i.e. over-water distance to Brisbane River) was set as a

covariate. Impacted sites (that changed within 2 years of the flood) were then analyzed separately with three-way PERMANOVA to compare responses of impacted reserve and fished reefs. The factors were: year (fixed orthogonal factor), site (random factor), and protection (fixed orthogonal factor). *A posteriori* pair-wise tests were used to interrogate annual within-location variation following PERMANOVA. Canonical analysis of principal coordinates (CAP) was then used to visualize the results of pair-wise tests following PERMANOVA, and illustrated strong differences among treatments with a small number of principal coordinates (δ^2: 0.71 − 0.95, *m*: 3 − 7) (Anderson & Willis, 2003). CAP provides flexible and meaningful constrained ordination of multivariate points by reference to explicit *a priori* hypotheses, and can therefore uncover patterns that are masked in unconstrained MDS ordination. It incorporates principal coordinate analysis (PCO, a metric MDS), followed by canonical discriminant analysis (CDA), to distinguish between group structure in the ordination space. Pair-wise test results are illustrated over ordinations using dashed lines to delineate coherent sample groups. Similarity Percentage contribution (SIMPER) analyses were used to identify coral genera responsible for differences in responses of reserve and fished reefs. All multivariate analyses were based on Euclidean (log x + 1) similarity measures, and performed using PRIMER.

Relationships between changes in coral assemblages over time and variation in ecological metrics and flood impact variables were examined using RELATE and BEST analyses. RELATE tests for correlation in the structure of different multivariate resemblance matrices (in this case between coral assemblage composition and both ecological metrics and physical impact variables) on the basis of spearman correlation tests. BEST is essentially a permutational nonparametric multivariate alternative to multiple regression, which identifies the environmental variables that best explain patterns of similarity in biotic assemblages. BEST analyses were used to identify the ecological metrics or impact variables with strongest correlation with temporal changes in coral assemblages (Clarke *et al.*, 2008). A detailed description of each multivariate analysis is provided in Appendix S1.

Mangrove-reef connectivity can affect reserve performance in Moreton Bay, and the potential effect of the reserve-connectivity interaction (on fish and coral recruits) was evaluated using asymmetrical ANOVA (Olds *et al.*, 2012a). Two-way analyses were performed to examine variation in fish density and three-way analyses were conducted for recruit density. The factors were connectivity (fixed orthogonal factor), site (random orthogonal factor), and year (fixed orthogonal factor used only in recruit analyses). Data were ln(x + 1) transformed to improve heterogeneity of variance. *Post hoc* Tukey's tests were used to differentiate significant means.

Results

Flood impacts on coral assemblages

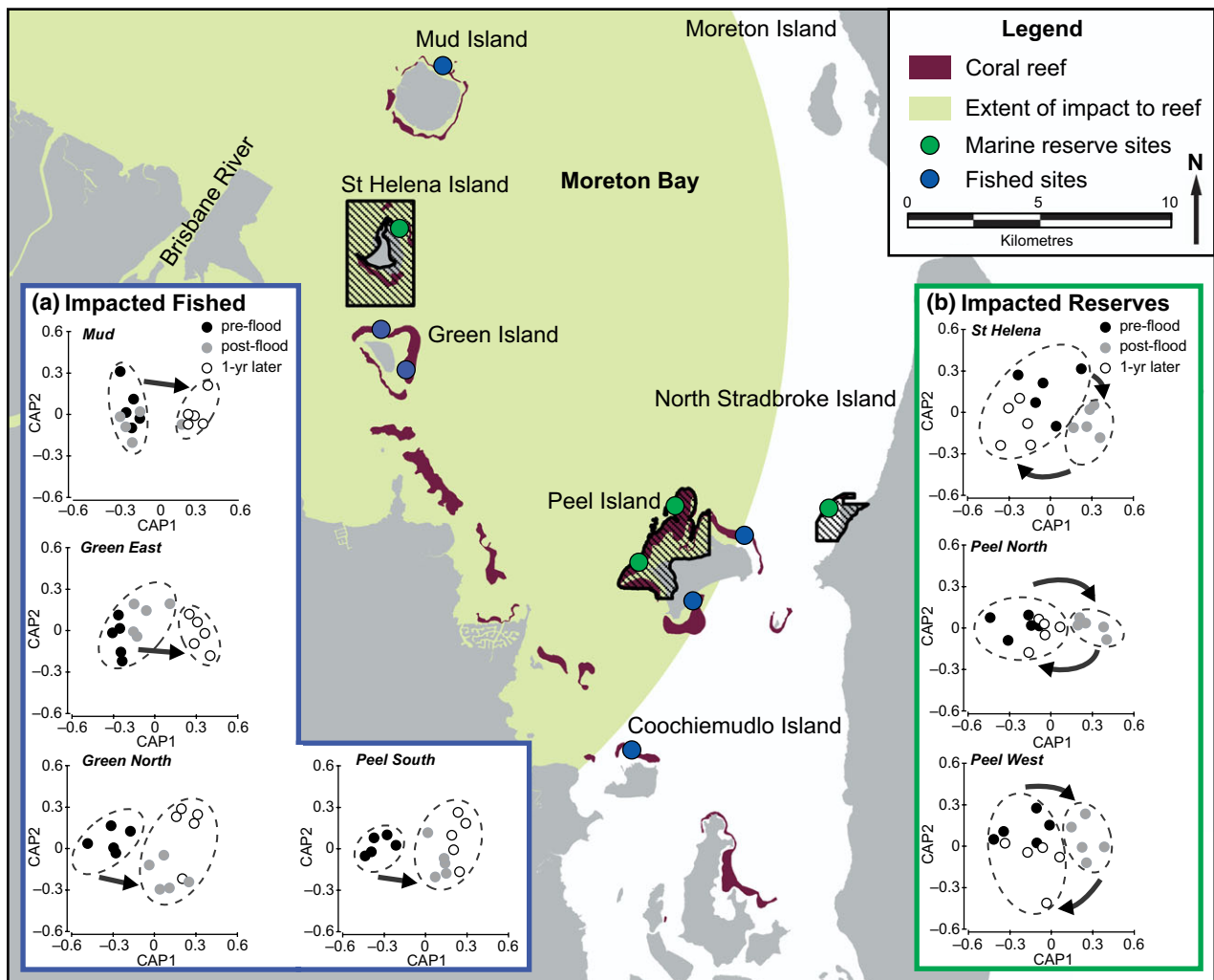The Brisbane River flood impacted coral reefs up to 30 km from the river mouth (Fig. 1, Tables S1 and S2

Fig. 1 The 2011 flood impacted reefs in Moreton Bay up to 30 km from the river. Three impacted sites (St Helena, Peel North, and Peel West) were inside reserves and four were open to fishing (Mud, Green East, Green North, and Peel South). Assemblage composition remained different after flooding at fished reefs (a), whilst reserve reefs recovered (b). Canonical analysis of principal coordinates (CAP) ordinations illustrate variation in assemblage composition; dashed lines delineate coherent groups ($P < 0.05$) defined by pairwise tests following PERMANOVA (Table S1 in Appendix S2). Impact extent is based on effects on reefs (Table S1 in Appendix S2) and water quality (Table S2 in Appendix S2). (Color in the online version)

in Appendix S2). Three impacted reefs (St Helena, Peel North, Peel West) were inside marine reserves and four impacted reefs were open to fishing (Mud, Green East, Green North, Peel South) (hereafter termed reserve and fished reefs) (Fig. 1, Table S1 in Appendix S2). Three other reefs (Coochiemudlo, Myora, Peel East) were not impacted by the flood (Fig. 1, Table S1 in Appendix S2). All reserve reefs had recovered within 1 year of the flood, whereas all fished reefs had not recovered one year postflood (Fig. 1, Table S3 in Appendix S2). Impacts to fished reefs occurred over two different timescales. Two fished reefs (Green North and Peel South) were impacted immediately, whilst impacts were not detected at the remaining two reefs (Mud and

Green East) until one year later (Fig. 1, Table S3 in Appendix S2). Losses of corals from three genera (*Cladiella*, *Goniopora*, and *Favia*) were responsible for >90% of annual variation on fished reefs, whilst changes in the cover of six genera (*Acanthastrea*, *Cladiella*, *Cyphastrea*, *Favia*, *Goniastrea*, and *Sansibia*) were responsible for >90% of annual variation on reserve reefs (Table S4 in Appendix S2). In addition to these assemblage level impacts, hard coral cover declined at one fished reef (Mud Island) and soft coral cover declined across the entire bay (Table S5 in Appendix S2).

Studies of spatial patterns in ecology can only infer causality after first testing and falsifying potential alternative explanations, and we verified that the observed

flood impacts were not explained by covariation of assemblage sensitivity or the severity of flood conditions experienced. Fished reefs did not support more sensitive coral assemblages than reserve reefs prior to the flood, nor were fished reefs closer to the river mouth, or subjected to more severe flood conditions than reserve reefs (Table 1).

Relationship between coral assemblages, ecological metrics and flood impacts

Changes in the composition of coral assemblages at fished reefs were correlated with physical impact variables, whereas variation in assemblage composition at reserve reefs was correlated with ecological variables (Table 2). For fished reefs, assemblage changes were best explained by water quality variables (i.e. turbidity and total phosphorus), whereas on reserve reefs, assemblage variation was best explained by the ratio of macroalgae to hard coral (Table 2). This suggests that stabilizing ecological processes may have been stronger on reserve reefs than fished reefs. The cover of sediments deposited over coral was also important on both reserve and fished reefs (Table S5 in Appendix S2).

Marine reserve effects on ecosystem processes

Several key ecological metrics differed between reserve and fished reefs (Fig. 2). The ratio of macroalgae to hard coral cover remained constant at reserve reefs during this study, but declined after the flood at fished reefs before increasing to approximately 2.5 × preflood levels (Fig. 2, Table S5 in Appendix S2). This followed the response of macroalgae (primarily, *Sargassum*, *Lobophora*, and *Padina*), not corals (Table S5 in Appendix S2). Variation in the response of reserve and fished reefs corresponds to preflood differences in herbivorous fish populations. The biomass of roving grazers (primarily,

Scarus ghobban and *Prionurus microlepidotus*), which consume turf algae, was greater on reserve than fished reefs. The biomass of roving browsers (primarily *Siganus fuscescens*), which consume fleshy macroalgae, however, was influenced synergistically by connectivity between reserves and mangroves. These fish visit mangroves on tidal feeding migrations and their biomass was greatest on reserve reefs near mangroves (Fig. 2) (Olds *et al.*, 2012a). The density of coral recruits varied between pre- and postflood samples, but was also always greater on reserve reefs near mangroves (Fig. 2) (Table S7 in Appendix S2).

Discussion

Promoting resilience is now a common objective for nature reserves, but their capacity to help ecosystems withstand external disturbance remains unproven, and is frequently debated (Cote & Darling, 2010; Mora & Sale, 2011). Our results show that coral reefs in marine reserves resisted the impact of a major flood, whereas similar fished reefs did not. We postulate that these different response trajectories may reflect a higher inherent ecological resilience of reserve reefs. Indeed, changes in assemblage composition at fished reefs were correlated with physical impact variables (primarily water quality), whereas variation in the composition of corals on reserve reefs was correlated with ecological variables. Corals in reserves were slightly overgrown by macroalgae for a short period, but it was no longer present 1 year after the flood. In contrast, corals on fished reefs were slowly overgrown by macroalgae, which remained abundant (at 2.5 × preflood levels) one year after the flood. The reason for delayed algal growth at fished reefs remains unclear, but it was presumably a lagged response to high initial sediment loads followed by improved water clarity (and growing conditions) after the flood plume passed.

Table 1 Potential alternative explanations for reduced impacts on reserve reefs

Potential Alternatives	Test	Result	Decision
1. Fished reefs were more sensitive than reserve reefs before the flood.	PERMANOVA using preflood (2010) coral assemblage data.	No difference ($P = 0.400$)*	Reject
2. Fished reefs were more severely impacted by the flood than reserve reefs.	PERMANOVA using data on proximity to river mouth.	No difference ($P = 0.656$)*	Reject
	PERMANOVA using postflood (2011) water quality and sedimentation data to quantify magnitude of impact.	No difference ($P = 0.450$)*	
	PERMANOVA using probable duration of depressed salinity (based on residency time) to quantify duration of impact.	No difference ($P = 0.841$)*	

*See Appendix S1 for methods and Table S8 in Appendix S2 for results.

Table 2 Relationships between temporal changes in assemblage composition, ecological metrics and physical impact variables on reserve and fished reefs. Values (*P* and *Rho*) are results of RELATE comparing resemblance matrices (based on Spearman correlation) and BEST analyses to identify the most important predictor variables

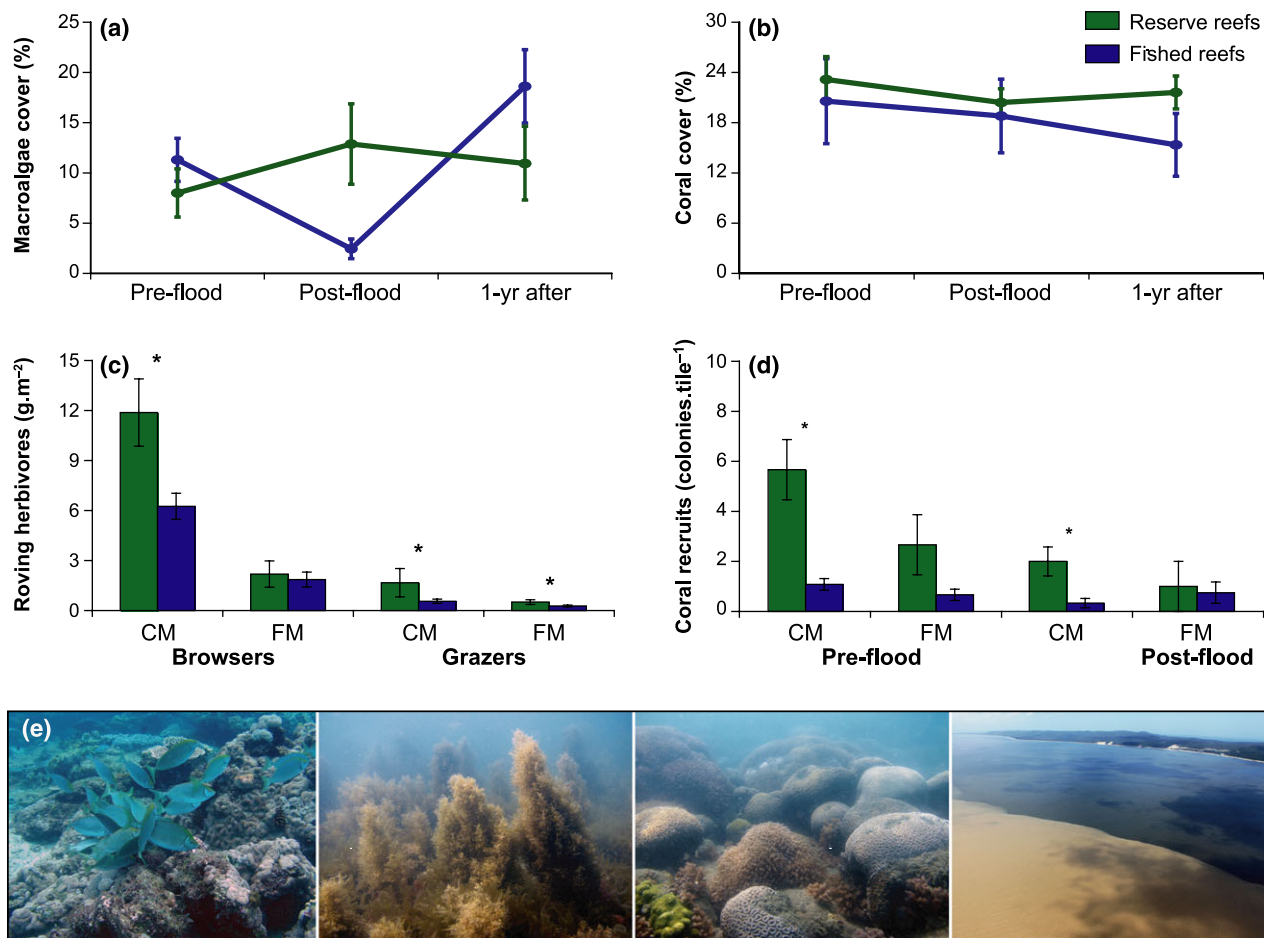| Impacted Sites	Reserve reefs		Fished reefs	
	P	*Rho*	*P*	*Rho*
Ecological variables	0.001	0.50	0.366	0.02
Impact variables	0.240	0.04	0.002	0.19
Best predictors	Macroalgae: hard coral (*P* = 0.010, *Rho* = 0.53)		Turbidity, total phosphorus (*P* = 0.010, *Rho* = 0.42)	

Fig. 2 Ecological processes and the cover of macroalgae (a) and hard coral (b) on marine reserve and fished reefs (Table S5 in Appendix S2). Before the flood, the biomass of grazing herbivorous fish was greater on reserve reefs, while browsing herbivorous fish biomass was higher on reserve reefs close to mangroves (c). Coral recruitment was greater on reserve reefs close to mangroves both pre and postflood (d). Data are means ± SEM. * significant differences between reserve and fished reefs (identified by Tukey's *post hoc* tests). The positive effect of reserves on herbivorous fish reduced macroalgae cover and enhanced coral recruitment and the capacity of reefs to absorb land-based disturbances (e). CM, reefs close to mangroves; FM, reefs far from mangroves. (Color in the online version)

We suggest that the positive effect of reserves on herbivore biomass, and the influence of herbivory on macroalgae and coral recruitment dynamics (Mumby *et al.*, 2007; Stockwell *et al.*, 2009; Olds *et al.*, 2012a), can enhance the capacity of reefs to absorb major regional-scale disturbances (like floods), and may thereby improve their ecological resilience. This result provides empirical evidence for the hypothesis that reserves may

help maintain ecosystem resilience (Bengtsson *et al.*, 2003; Cote & Darling, 2010; Olds *et al.*, 2012a), and supports the incorporation of resilience into spatial conservation planning (Nyström & Folke, 2001; Fischer *et al.*, 2009; Cumming, 2011). It also appears to contradict research showing little effect of marine reserves on the recovery of reefs from global-scale disturbances (e.g., temperature induced coral bleaching) (Graham *et al.*, 2008; Selig & Bruno, 2010; Selig *et al.*, 2012). However, faster rates of coral recovery from bleaching have been documented in some reserves in the Seychelles (Wilson *et al.*, 2012). Reserves have also been shown to enhance the resistance of temperate reef communities to changes in biodiversity, which are associated with thermal range shifts (Bates *et al.*, 2014).

Reef communities are under stress from the cumulative impacts of a variety of different perturbations, which operate at different scales (Darling *et al.*, 2010; Graham *et al.*, 2011; Halpern *et al.*, 2013). Studies examining the response of reef communities to similar regional-scale disturbances (e.g., sedimentation, crown-of-thorns starfish outbreaks, hypoxia) have produced mixed results (McCook *et al.*, 2010; Micheli *et al.*, 2012; Halpern *et al.*, 2013). For example, marine reserves appear to have had little effect on the resilience of reefs to sedimentation impacts (associated with logging in adjacent catchments) in the Solomon Islands (Halpern *et al.*, 2013). On the other hand, reserves seem to have increased resilience to outbreaks of crown-of-thorns starfish (a major cause of regional coral mortality) on the Great Barrier Reef, with reserve reefs consequently supporting higher coral cover than fished reefs (McCook *et al.*, 2010). Reserves also increased the resilience of reef populations to climate-driven hypoxia events in Mexico (Micheli *et al.*, 2012). At a global scale, however, reserves seem to have little effect on the recovery of coral reefs from a variety of pulse disturbances (Graham *et al.*, 2011). The ability of reserves to help ecosystems withstand perturbation may, therefore, depend on the type, severity and scale of disturbance, as well as their capacity to enhance ecological processes that promote resistance to, or recovery from, the type of perturbation experienced. Consequently, reserves might be expected to influence the resilience of ecosystems to local and regional-scale climate-related disturbances (e.g., severe weather events), but not to global-scale events (e.g., rising temperatures, ocean acidification). To evaluate the effect of scale and provide clear empirical tests of the ability of reserves to promote ecological resilience, research must focus on understanding the dynamic relationship between perturbation, stabilizing ecological processes and ecosystem response (Thrush *et al.*, 2009; Nyström *et al.*, 2012; Hughes *et al.*, 2013; Mumby *et al.*, 2013a).

Coral reefs in Moreton Bay have been degraded by a history of eutrophication and sedimentation, by heavy fishing pressure, the harvesting of herbivorous fish and the extraction of coral for construction materials (Pandolfi *et al.*, 2003; Lybolt *et al.*, 2011; Olds *et al.*, 2012a). They have also been sculpted by the impact of previous floods, which have altered the composition and distribution of coral assemblages (Wallace *et al.*, 2009; Lybolt *et al.*, 2011). This disturbance history may well have selected for ecological resistance in corals on extant reefs across the entire ecosystem (Wallace *et al.*, 2009), a feature that could prove common to reefs that persist under conditions close to thresholds for coral survival (Perry & Smithers, 2011; Beger *et al.*, 2014). The effects of marine reserves on key ecological processes may have strengthened this capacity for resistance and improved the capacity of individual reefs to withstand local disturbances. Furthermore, high-latitude reefs like those in Moreton Bay are now viewed as potential refuges for tropical species threatened by climate change (Lybolt *et al.*, 2011; Beger *et al.*, 2014; Graham *et al.*, 2014). The capacity of subtropical marine reserves to protect coral reef seascapes against regional-scale climate-related disturbances (e.g., severe weather events) might, therefore, also enhance the suitability of these ecosystems as refugia for migrating tropical species.

Our findings show that reserves can successfully enhance the capacity of a degraded ecosystem to withstand external disturbance and support further optimization of spatial conservation planning for resilience (Bengtsson *et al.*, 2003; Fischer *et al.*, 2009). The capacity of nature reserves to promote resistance to regional-scale external disturbance has important implications for conservation in marine, freshwater and terrestrial ecosystems, and illustrates the importance of local natural resource management against a backdrop where global changes threaten the continued functioning of ecosystems.

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Supporting Information

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

Appendix S1. Supporting methods.
Appendix S2. Supporting tables.