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LETTER

Marine protected areas increase resilience among coral reef communities

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Abstract

With marine biodiversity declining globally at accelerating rates, maximising the effectiveness of conservation has become a key goal for local, national and international regulators. Marine protected areas (MPAs) have been widely advocated for conserving and managing marine biodiversity yet, despite extensive research, their benefits for conserving non-target species and wider ecosystem functions remain unclear. Here, we demonstrate that MPAs can increase the resilience of coral reef communities to natural disturbances, including coral bleaching, coral diseases, *Acanthaster planci* outbreaks and storms. Using a 20-year time series from Australia's Great Barrier Reef, we show that within MPAs, (1) reef community composition was 21–38% more stable; (2) the magnitude of disturbance impacts was 30% lower and (3) subsequent recovery was 20% faster that in adjacent unprotected habitats. Our results demonstrate that MPAs can increase the resilience of marine communities to natural disturbance possibly through herbivory, trophic cascades and portfolio effects.

Keywords

Acanthaster planci, benthos, biodiversity, bleaching, crown-of-thorns starfish, cyclone, disturbance, fish, Great Barrier Reef, marine reserves.

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INTRODUCTION

Accelerating rates of biodiversity loss in recent decades (Pimm *et al*. 2014) and the lack of effective action to reduce global warming has increased the need for effective management that can improve ecosystem resilience – the ability to resist and recover from disturbance. For marine ecosystems, no-take marine reserves or marine protected areas (MPAs) are a commonly applied management tool that is thought to be effective in conserving biodiversity and enhancing the biomass of fished species provided certain conditions of design, management and enforcement are met (Cinner *et al*. 2012; Edgar *et al*. 2014). Yet the assumption that, by removing fishing pressure, MPAs also promote ecosystem resilience (Mora *et al*. 2006) remains controversial (McClanahan *et al*. 2012a; Graham *et al*. 2013), with examples of both success (Mumby & Harborne 2010; Emslie *et al*. 2015) and failure (Mora & Sale 2011) of MPAs to mitigate the effects of natural and anthropogenic disturbances. On coral reefs, some of the most diverse and threatened ecosystems on Earth (Knowlton *et al*. 2010; Fisher *et al*. 2011; Caley *et al*. 2014), protection of herbivorous fish that graze on macroalgae may contribute to faster coral recovery in MPAs (Mumby & Harborne 2010) and ultimately benefit a wide range of taxa through the indirect and delayed effects of trophic cascades (Babcock *et al*. 2010). However, empirical evidence that MPAs also benefit these other benthic organisms remains very limited (but see Micheli *et al*. 2012; Selig & Bruno 2010). Therefore, whether coral reef MPAs can successfully mitigate the effects of multiple disturbances remains controversial and their role in promoting coral reef resilience remains unresolved.

Australia's Great Barrier Reef (GBR) is the world's largest coral reef ecosystem with global significance recognised by the IUCN World Heritage List (Wilkinson 2008). The GBR is subject to a range of disturbances including tropical storms, coral bleaching events, outbreaks of the coral predator *Acanthaster planci* Linnaeus 1758 (crown-of-thorns starfish) and coral diseases (Osborne *et al*. 2011; De'Ath *et al*. 2012) that continue to degrade its condition. The number of reefs impacted annually by disturbance has also increased in recent decades, primarily as a result of major storms affecting the central and southern sections of the GBR (Figs 1 and 2).

Using a unique long-term and broad-scale set of fish (215 species) and benthic (34 growth forms) community composition data that captures multiple disturbances across 150 000 km^2 of reef (Sweatman *et al*. 2008), we explored differences in community resistance and recovery between 20 reefs within MPAs and 26 reefs open to fishing between 1993 and 2013. Because the status of five reefs changed from open to MPA during this period, we were also able to study changes in resilience associated with a change in protection status. We quantified temporal change in community composition (Mellin *et al*. 2014) using a multivariate, temporally lagged index of community dissimilarity and compared the timing and magnitude of its responses to disturbance using hierarchical linear models.

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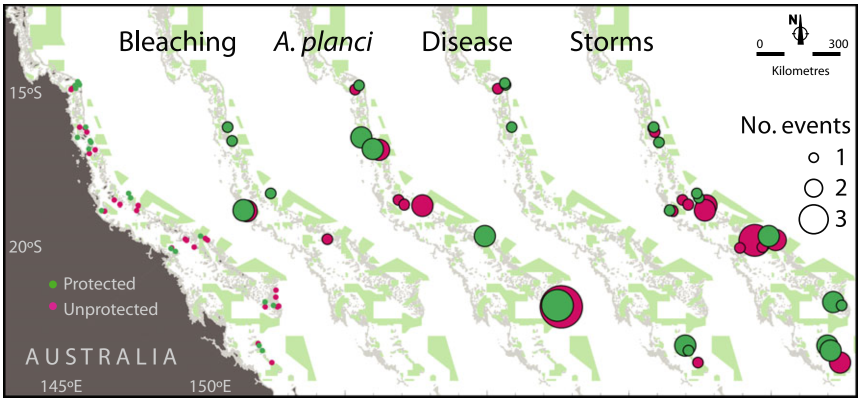

Figure 1 Reef protection status and disturbance history on the Great Barrier Reef (GBR), Australia. The left hand-side map shows the locations of study reefs (green dots: marine protected areas [MPAs]; purple dots: non-MPAs) and the location of the main MPAs (green polygons). The numbers of disturbances (Osborne *et al.* 2011) per reef over the study period (1993–2013) are indicated by the sizes of the symbols, with the colour indicating reef status. For clarity, each disturbance type is plotted on a separate map of the reefs of the GBR.

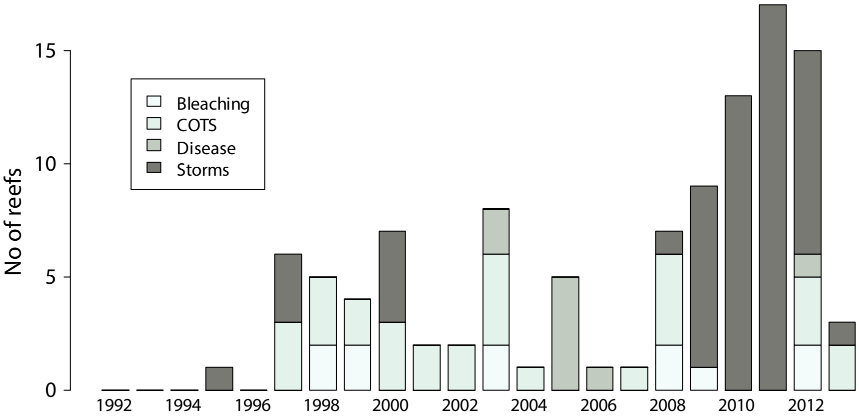

Figure 2 Number of surveyed reefs impacted by each type of disturbance in each year.

MATERIALS AND METHODS

Study reefs

Australia's Great Barrier Reef (GBR) consists of more than 2900 individual reefs extending over 2300 km between 9 and 24 °S latitude (Fig. 1). Reef communities of the GBR have been monitored yearly between 1993 and 2005, and then biennially thereafter, by the Australian Institute of Marine Science's (AIMS) Long-Term Monitoring Program (LTMP) (Sweatman *et al.* 2008). As part of the LTMP, fish and benthic assemblages have been surveyed on 46 reefs in six latitudinal sectors (Cooktown-Lizard Island, Cairns, Townsville, Whitsunday, Swain and Capricorn-Bunker) spanning 150 000 km^2 of the GBR (Fig. 1). In each sector (with the exception of the Swain and Capricorn-Bunker sectors) at least two reefs were sampled in each of three shelf positions (i.e. inner, mid- and outer). These 46 reefs included 20 reefs within MPAs, including five that were first protected after 2004, and 26 reefs open to fishing between 1993 and 2013. Within the five reefs that were protected after 2004, two reefs (i.e. Langford and Bird Island reefs) included zones of different protection status, with the LTMP sites located in MPAs.

Disturbance data

We classified disturbances into four categories (i.e. coral bleaching, *A. planci* outbreaks, coral disease or storms) following Osborne *et al.* (2011) based on visual assessment by experienced divers during reef-scale manta tow and intensive SCUBA surveys. Each disturbance was identified by distinctive and identifiable effects on corals, such as the presence of *A. planci* individuals or feeding scars, or dislodged and broken coral indicative of storm damage (Osborne *et al.* 2011). Between 1993 and 2013, seven reefs were impacted by coral bleaching, 23 by *A. planci* outbreaks, seven by coral disease and 34 by storms (i.e. tropical cyclones or sub-cyclonic storms) (Fig. 2). Disturbance severity was estimated as the mean percent change in live and dead coral cover following disturbance across all transects of the same reef (calculated as the difference in percent coral cover before and after disturbance) (De'Ath *et al.* 2012).

Survey methods and data collection

At each reef, three sites separated by > 50 m were selected for sampling within a single habitat on the reef slope (the first stretch of continuous reef on the northeast flank of the reef, excluding vertical drop-offs). Within each site, five permanently marked 50-m-long transects were deployed parallel to the reef crest, each separated by 10–40 m along the 6–9-m-depth contour. Percentage cover of benthic categories (see Table S1) were estimated for each transect using point sampling of a randomly selected sequence of images (Jonker *et al.* 2008). Within these transects, abundances of 215 fish species representing 10 families (Sweatman *et al.* 2008) were also estimated each year. Small site-attached species such as damselfishes (Pomacentridae) were counted in a 1-m-wide strip and a 5-m-wide transect was used for larger, mobile species (see Halford & Thompson 1996 for detailed methods). Only fishes > 1-year old were recorded, these being distinguished from younger fish by their size and coloration. Excluding younger fish ensured that trends in community structure were buffered from inherent recruitment fluctuations.

Temporal dissimilarity in community composition and data management

For each reef, among-year dissimilarities were calculated using abundance-based Bray-Curtis dissimilarity. We defined the *i*th lagged dissimilarity as the Bray-Curtis dissimilarity in community structure between years $t-1$ and $t+\mathrm{i}$ ($\Delta_{t\text{-}1,t+\mathrm{i}}$), which we matched to binary covariates for the occurrence of bleaching, *A. planci* outbreaks, disease or storms in year *t*, and the reef closure status in year *t*. Separate datasets were collated for fishes (using fourth-root transformed individual abundances) and benthic assemblages (using square-root transformed percent cover) (Emslie *et al.* 2010). Pairwise dissimilarities were calculated using the function '`vegdist`' of the `{vegan}` R package (R Development Core Team 2013).

Modelling

The modelling followed three main steps: (1) we first compared the level of temporal stability in benthic and fish community structure on MPA vs. non-MPA reefs using non-metric multidimensional scaling (nMDS; Clarke 1993); (2) we then determined the temporally-lagged effects of each type of disturbance on both benthic and fish community structure using hierarchical, generalised linear mixed-effect models (GLMM; Gelman & Hill 2007); (3) finally, we identified the fish species and benthic growth forms that were primarily responsible for the dissimilarity in community structure after each type of disturbance using a similarity percentage analysis (SIMPER; Clarke & Warwick 2001).

We compared the magnitude of temporal dissimilarity in community structure on MPA vs. non-MPA reefs using nMDS. For both fish and benthic assemblages, we defined a sample by the community structure observed at a particular reef in a particular year, where samples-by-species matrices were transformed to Bray-Curtis dissimilarity matrices and used as an input for nMDS. From this, we compared the overall temporal stability of benthic and fish assemblages on MPA vs. non-MPA reefs using distance and area-based metrics of ordination scores (Layman *et al.* 2007) including range (RA; maximum distance between dots), total area (TA; area of the polygon delimited by dots), mean distance to centroid (CD; average distance between dots and polygon centroid) and mean year-to-year distance (YD; average distance between each dot and the next one in the time series). In addition, following Anderson & Thompson (2004), we also included the average distance to the baseline centroid (BD; average distance between each dot and the initial community composition). We compared the value of these five metrics between MPA and non-MPA reefs, and between infrequently disturbed (≤ 3 disturbance events, $N = 3$ being the median number of disturbances) and frequently disturbed reefs (> 3 disturbance events) using a Student–Newman–Keuls post hoc pairwise comparison test ('`snk.test`' in `{GAD}`) (R Development Core Team 2013) to determine their relative temporal instability.

To estimate the average effect size of each disturbance type on benthic and fish community structure, we modelled the dissimilarity between years $t-1$ and $t+\mathrm{i}$ ($\Delta_{t\text{-}1,t+\mathrm{i}}$) as a function of disturbance type (bleaching, *A. planci* outbreaks, disease or storms; coded as binary covariates) and closure status (binary), in year *t*, using GLMMs with a *Reef* random effect to account for the non-independence of observations at a single reef. This procedure assumed that disturbances were equally severe between MPA and non-MPA reefs (Fig. S1). We thus included, as fixed effects, the mean percent change in live and dead coral cover as proxies for disturbance severity (Fig. S1), and the reef-centred initial live and dead coral cover as proxies for initial reef condition (Fig. S2). A candidate model set comprised of 18 models included all linear combinations of disturbances and a null (intercept-only) model. For years towards the end of the time series, some of the lagged data were unavailable (i.e. years post-disturbance beyond the end of the time series) and were thus not fully accounted for. We could not include potential interactions between disturbances because of insufficient observations of co-occurring disturbances. In addition, we could not distinguish infrequently disturbed (≤ 3 disturbance events, corresponding to the median) vs. frequently disturbed reefs (> 3 disturbance events) while fitting the models, because of missing covariate combinations in each of these categories; instead, we included the total number of disturbances at each reef prior to year *t* as a fixed effect in our models. We assumed a Normal error distribution with a log-link and verified this assumption through the normality of residuals (Breslow 1996). We assessed GLMM performance using percent deviance explained (De) to provide an index of the model's goodness-of-fit (Crawley 2005) and used Akaike's information criterion corrected for small sample sizes (AIC_c) to assign relative strengths of evidence to the different competing models (Burnham & Anderson 2002). We ranked models by increasing $w\mathrm{AIC}_c$ (AIC_c weights, indicative of model predictive accuracy) and used them to calculate weighted-average model predictions of disturbance effect sizes according to each temporal lag, both for benthic and for fish assemblages, and on MPA vs. non-MPA reefs. Temporal trends (envelopes) and predicted time to recovery (partial effect = 0) were estimated using local polynomial (`loess`) regression.

We identified the benthic categories and fish species mostly responsible for post-disturbance dissimilarity in community structure on MPA vs. non-MPA reefs using SIMPER analysis (Clarke & Warwick 2001). For this analysis, we considered the temporal lag at which dissimilarities were the greatest for both benthic and fish assemblages. For each disturbance event and according to each temporal lag, the percentage contribution of each species to the overall dissimilarity $\Delta_{t\text{-}1,t+\mathrm{i}}$ was estimated, and recorded as positive if it corresponded to an increase in abundance (or percentage cover), negative for a decrease. Percentage contributions were weighted by each species' relative abundance across all reefs and years, averaged across the multiple events to define species-specific mean percentage contributions to the dissimilarity observed following each type of disturbance. We then compared these species-specific percentage contributions (mean and 95% confidence interval) on MPA vs. non-MPA reefs.

Finally, we tested the null hypothesis that the diversity and structure of fish and benthic assemblages did not differ between MPA and non-MPA reefs by (1) considering different disturbance regimes (i.e. reefs exposed to ≤ 3 disturbance events; reefs exposed to > 3 disturbance events) and (2) using a permutational multivariate analysis of variance (Anderson 2001), one for each disturbance regime, with reef protection status as the covariate and $n = 999$ permutations.

RESULTS

Based on year-to-year trajectories in community composition (Fig. 3), fish and benthic assemblages were more stable on reefs inside MPAs than on non-MPA reefs (Fig. 4), with smaller deviations in year-to-year community change over 20 years (*t*-test; $P < 0.001$). Strikingly, this greater stability within MPAs occurred despite a greater number of disturbances within them compared to non-MPAs (*t*-test; $P = 0.048$) and comparable loss of live coral (*t*-test; $P > 0.05$; except following disease that resulted in higher loss of live coral cover in MPAs; $P = 0.008$) (Fig. S1). Spatial and environmental characteristics such as geographical location, reef area or isolation were similar in both MPAs and non-MPAs (*t*-test; $P > 0.05$; Fig. S3). Based on the most extreme changes in community composition observed over the entire time series

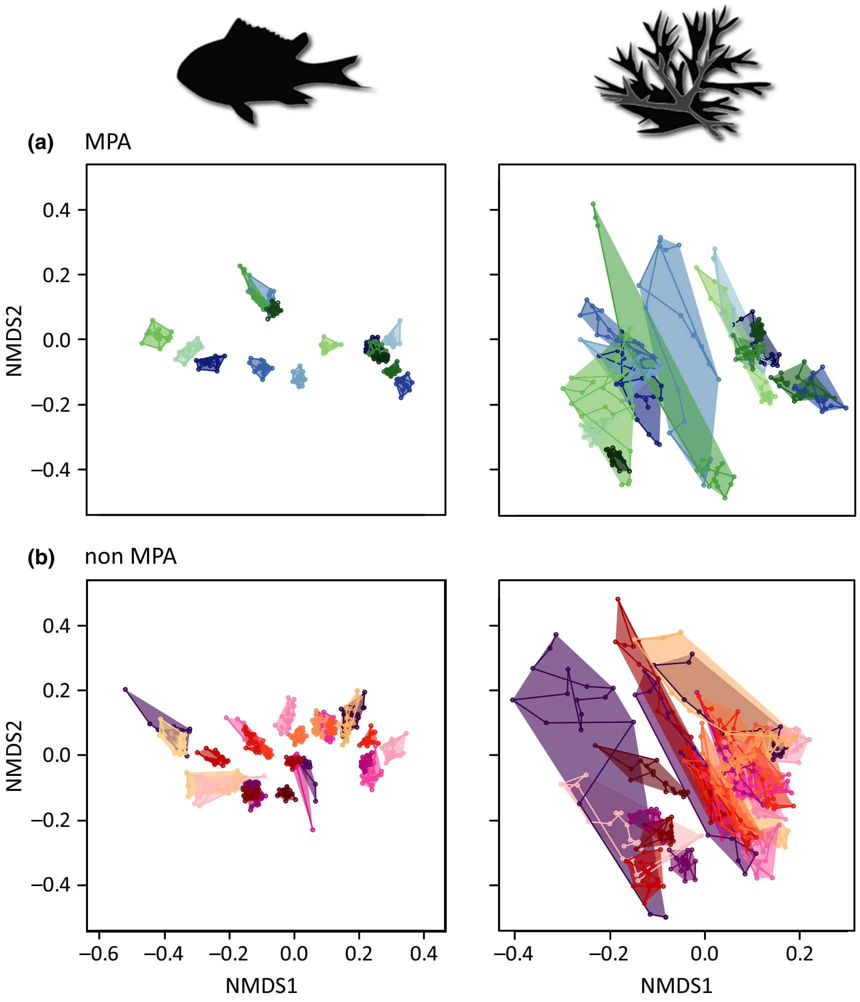

Figure 3 Year-to-year trajectories of fish (left) and benthic (right) assemblage structure over the study period on MPA (top) and non-MPA reefs (bottom). Each colour represents a particular reef, and each dot the community composition at this reef in a given year based on non-metric multidimensional scaling (NMDS).

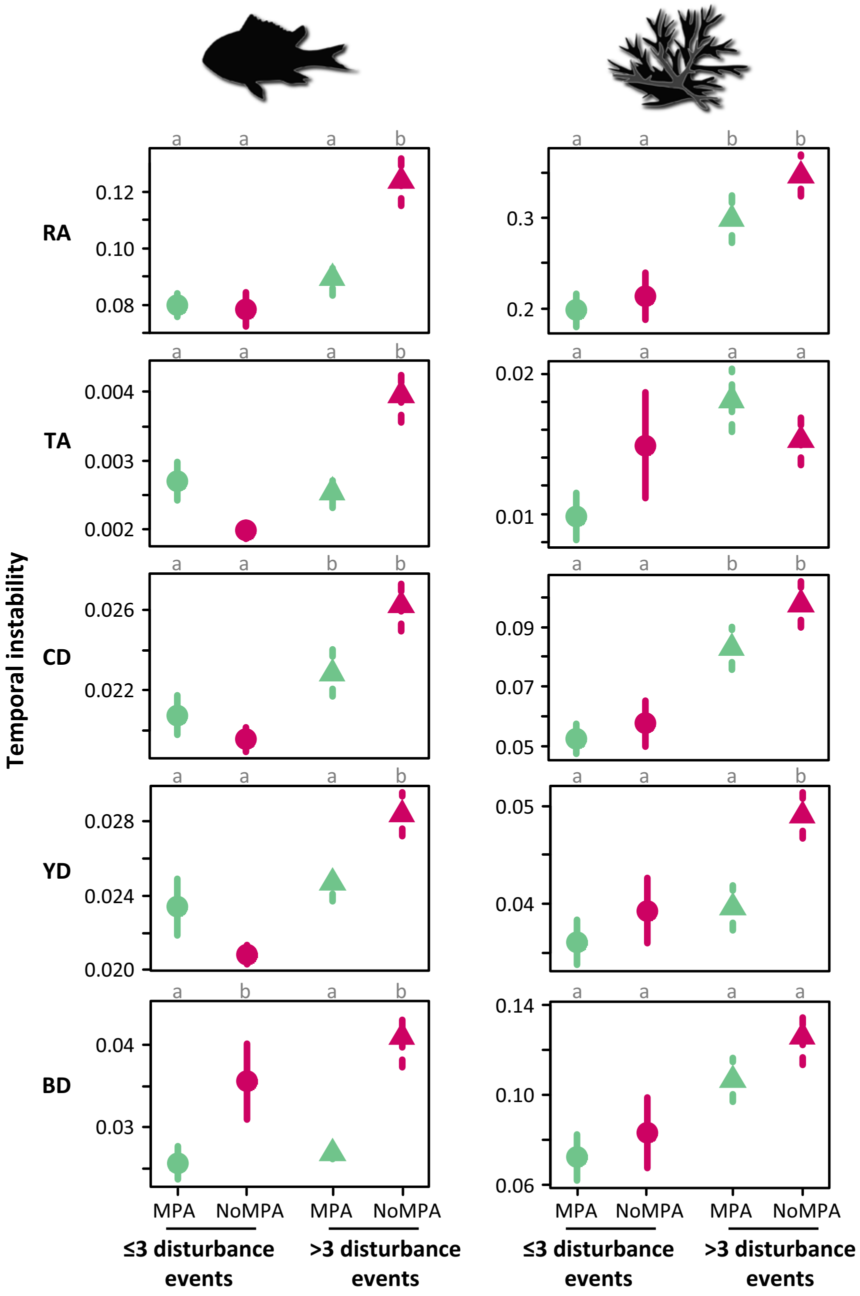

Figure 4 Temporal instability of fish and benthic assemblages in marine protected areas (MPA; green) vs. non-MPAs (purple) extracted from the non-metric multidimensional scaling. Instability metrics include the range (RA), the total polygon area (TA), the mean distance to centroid (CD; an index of departure from average community composition), the mean year-to-year distance (YD) and the average distance to the baseline centroid (BD; an index of departure from initial community composition), with error bars indicating standard deviation. Reefs exposed to > 3 disturbance events between 1993 and 2013 were considered frequently disturbed, those exposed to few disturbances less frequently disturbed. Grey letters (a and b) indicate groups that differ (Student-Newman-Keuls test; $P < 0.05$).

(range, *RA*), fish and benthic assemblages were 38 and 25% more stable in MPAs compared to non-MPAs, respectively, and 21 and 25% more stable based on year-to-year dissimilarities (*YD*) (Fig. 4). As expected, more frequently disturbed reefs (i.e. >3 disturbances between 1993 and 2013) were more temporally variable than less disturbed ones. As a result, the most temporally variable assemblages were typically observed on frequently disturbed, non-MPA reefs (Fig. 4). For fish in particular, the range (*RA*) and total area (*TA*) covered by community trajectories were greater on frequently disturbed non-MPA reefs, as was the average year-to-year dissimilarity in community composition (*YD*) (Fig. 4). For both fish and benthic assemblages we also observed (1) greater departures from the average community composition (centroid of the entire time series; *CD*) on frequently disturbed reefs, irrespective of reef protection status, and (2) greater departure from the baseline community composition (based on year one surveys; *BD*) on non-MPA reefs, irrespective of disturbance frequency (Fig. 4). Although the combined effects of reef protection and disturbance on benthic assemblages were less discernible than for fishes, there was greater year-to-year dissimilarity (*YD*) in benthic community composition on more frequently disturbed non-MPA reefs, in addition to higher values in dissimilarity metrics than on less frequently disturbed and non-MPA reefs (Fig. 4). Critically, positive effects of protection from fishing on resilience also became apparent among reefs that were initially unprotected but became an MPA during the course of this study, with substantial stabilisation of most fish and benthic assemblages following protection (Table S2).

Trajectories of community composition revealed that protection from fishing reduced temporally lagged effects of disturbance on community composition up to 5 years following disturbance (Fig. 5). In all cases, changes in community composition from their pre-disturbance state (partial effect = 0 on Fig. 5) were smaller on MPA reefs by 30% on average (range 10–52%), with similar rates of recovery to pre-disturbance composition. Subsequent recovery times to pre-disturbance states were 20% faster on average, and therefore, typically 1 year shorter on MPA compared to non- MPA reefs, irrespective of the type of disturbance impacting these reefs (Fig. 5). All types of disturbance resulted in loss of hard coral cover, mostly tabular and branching *Acropora spp.*, which was predominantly replaced by algal turfs (Fig. S4a, Table S1). The magnitude of these changes was generally greater on non-MPA reefs (Fig. S4a; open symbols showing greater relative changes without overlapping with closed symbols).

In addition to physical damage of the reef structure, disturbances also affected reef fishes reliant on corals for shelter, food or recruitment habitat. The greatest change in benthic community composition was observed on non-MPA reefs 1 year after bleaching events and *A. planci* outbreaks, and 2 years after storms (Fig. 5, upper panels). Notably, these effects were paralleled by associated fish assemblages (Fig. 5, lower panels). For example we observed the longest benthic recovery time after *A. planci* outbreaks (MPAs ~ 6.6 years, non-MPAs ~ 8.7 years; Fig. 5); after the same outbreaks, fish assemblages took 6 years to recover on MPA reefs but never fully recovered on reefs outside of MPAs. On these non-MPA reefs, the greatest changes in fish community composition were related to losses of corallivores and coral-associated planktivores or omnivores, with a moderate increase in the abundance of several herbivore and detritivore species (Fig. S4b, Table S3).

Together, reef protection status and disturbance explained approximately half of all the temporal changes observed in community composition across the entire time series, explaining up to 62% of the post-disturbance changes in benthic community composition (% deviance explained; range 51–62%; Table S4a) and 48% of those in fish community composition (range 45–48%; Table S4b). We found no effect of reef protection alone on the structure of fish or benthic assemblages, irrespective of the disturbance frequency ($P > 0.05$; distance-based permutational multivariate analysis of variance). Indeed, reef protection only explained 8% of the variation in benthic community structure and 9% for fishes. On

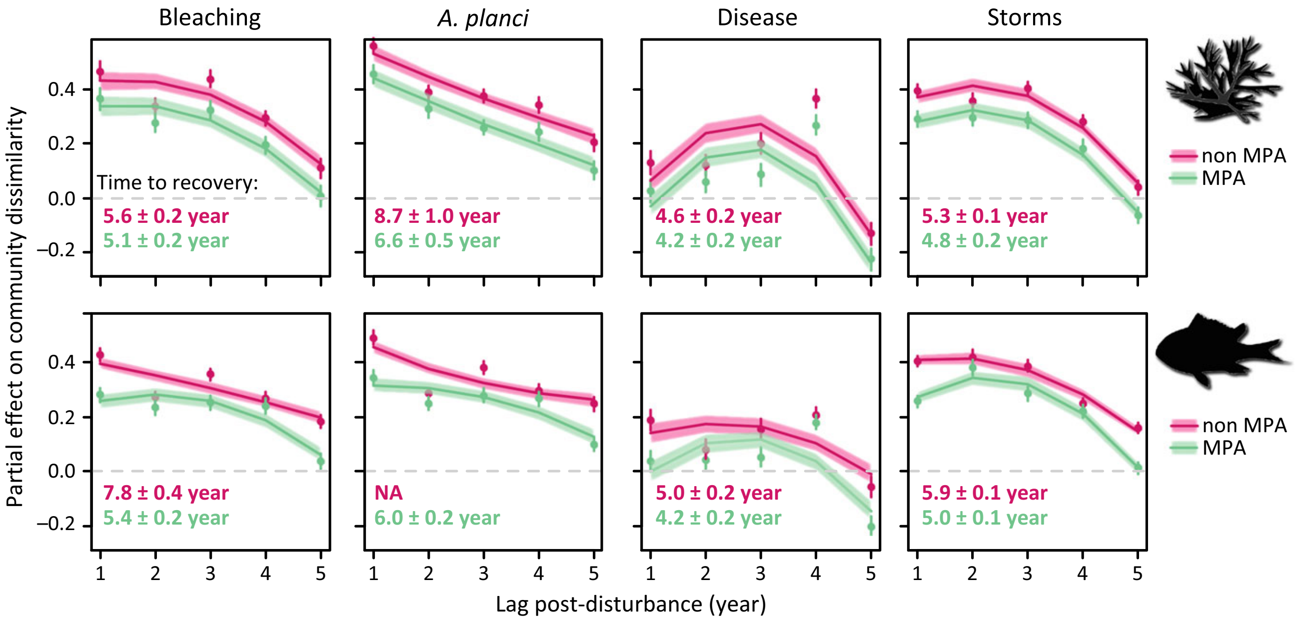

Figure 5 Temporally-lagged effects of multiple disturbance types on benthic (top) and fish (bottom) assemblages over 5 years following disturbances. Partial effect sizes were calculated using hierarchical linear models accounting for reef protection, disturbance severity and the number and cumulative effect of past disturbances for reefs located in marine protected areas (MPA; green) vs. non-MPA reefs (purple). Weighted-average predictions were calculated across the entire model sets based on model support (Table S4). Dots indicate the mean effect size and error bars show the standard deviation. The grey dotted line (partial effect = 0) represents no more dissimilarity with the pre-disturbance state than expected by chance. Negative values represent less dissimilarity with the pre-disturbance state than expected by chance. Temporal trends (envelopes) and predicted time to recovery (partial effect = 0) were estimated using loess regression. *Acanthaster planci* outbreaks are labelled *A. planci*.

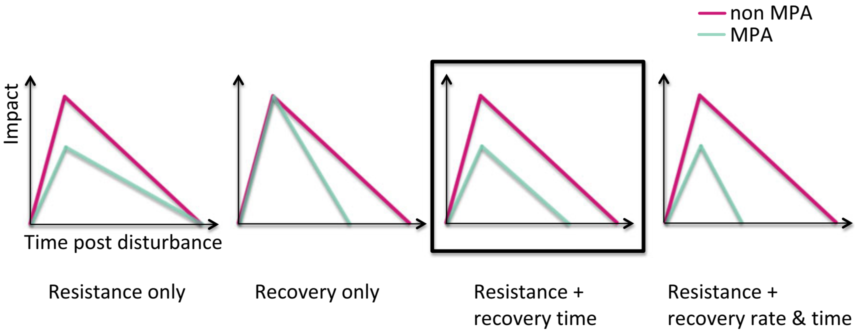

Figure 6 Schematic of the different components of resilience and corresponding post-disturbance impacts and community trajectories.

less frequently disturbed reefs, reef protection alone explained only 5% of the variation in benthic community structure and 3% for fishes.

DISCUSSION

Despite a linear decline in average coral cover on the GBR since 1994 (De'Ath *et al.* 2012), our results demonstrate that MPAs have increased both the resistance and recovery of coral reef community composition in response to a range of disturbances, on the shallow reefs of the Great Barrier Reef studied here. Protection from fishing was associated with reduced impacts over the 5 years following disturbance and these reef communities showed smaller excursions from their pre-disturbance composition with more rapid recovery. Although recovery rates were similar, higher resistance to disturbance in MPAs combined with similar recovery rates as in non-MPAs resulted in shorter recovery times (i.e. higher elasticity) within MPAs (Fig. 6). Although reef protection alone did not affect community composition, corroborating recent findings (Emslie *et al.* 2015), spatial turnover in community composition (β-diversity) has been shown to be higher in MPAs, resulting in more spatially heterogeneous communities on protected reefs (Mellin *et al.* 2014).

Dominant ecological mechanisms potentially responsible for the increased resilience observed in these MPAs include the roles of herbivory, trophic cascades and portfolio effects. First, increased grazing by herbivores in Caribbean MPAs generated substantial reductions in macroalgal cover that could promote subsequent recovery of coral on bare substrates (Mumby *et al.* 2006). Although we did not detect any difference in the number or diversity of herbivores between MPAs and non-MPAs, any variation in parameters we did not measure (e.g. herbivore biomass, grazing rates or home range) could have promoted greater grazing efficiency in the MPAs studied. Such variation, however, is unlikely to occur, since herbivores are not targeted on the GBR. Second, trophic cascades could be partly responsible for these results in that they generate increased predation of coral predators (Sweatman 2008). We found that the impact of *A. planci* was reduced in MPAs, and potential trophic cascades could have promoted invertebrates that prey on juvenile *A. planci*. The roles of trophic cascades remain, however, equivocal in tropical systems (Rizzari *et al.* 2015). Third, greater biodiversity can promote resilience by ensuring that a range of species perform each ecological function within a community (i.e. the portfolio effect) (Thibaut *et al.* 2012; Anderson *et al.* 2013). Although we found no differences in species richness (α-diversity) between MPA and non-MPAs, such differences in species turnover among reefs (β-diversity) have been associated with greater temporal stability in MPAs (Mellin *et al.* 2014) and could, therefore, also confer greater resilience to disturbance. Indeed, greater β-diversity in MPAs increases the odds that at least some communities will resist disturbances, and thereby act as refuges from which neighbouring patches can be replenished. Most conservation-planning algorithms maximise β-diversity indirectly by prioritising sites with the greatest species complementarity (Mellin *et al.* 2014). Therefore, it is very likely that MPA selection indirectly promoted spatial turnover and temporal stability – although many other ecological, social and economical factors were taken into consideration and could have blurred this picture. Lastly, MPAs can improve coral reef resilience by reducing the impacts of diseases associated with anthropogenically driven injury (Lamb *et al.* 2015) and human activities that reduce recruitment success in a range of reef organisms (Holles *et al.* 2013). Even though portfolio effects (i.e. β-diversity enhancing stability) seem the most likely cause of our observations here, the effects of these other ecological mechanisms may also have acted in some combination to increase the resilience of these coral reef communities in MPAs.

The processes underpinning resilience of coral reefs are complex, meaning that the effects of protection from fishing can be idiosyncratic and difficult to predict. For example following the 1998 mass coral bleaching event in the Western Indian Ocean, faster recovery of coral cover was observed within MPAs in the Seychelles (Wilson *et al.* 2012), yet in Kenya declines in coral assemblages were initially greater in MPAs than non-MPAs (Darling *et al.* 2013). These reefs were probably subject to greater fishing pressure prior to zoning than the GBR and thus might not be directly comparable to our study system, yet such variable responses underscore the importance of studying post-disturbance reef community dynamics, rather than just coral cover (Johns *et al.* 2014). Our results showed that, among coral growth forms, some (e.g. soft corals) were specifically vulnerable to a particular type of disturbance (e.g. bleaching and storms), whereas some others (e.g. tabular and branching *Acropora spp.*) were consistently vulnerable across disturbances, suggesting these taxa might be most at risk from cumulative impacts of successive disturbances. By studying community dynamics in this way, species likely to 'win' or 'lose' under different natural or anthropogenic disturbance regimes (Darling *et al.* 2013) can be identified, and understanding can be gained about the potential shifts of these communities to a greater representation of disturbance-tolerant species and faster return times to pre-disturbance community structure (Hoegh-Guldberg *et al.* 2007; Hughes *et al.* 2012).

Although MPAs are widely advocated for managing marine ecosystems (Lubchenco & Grorud-Colvert 2015), in many places they remain controversial (Christie 2004; Beddington *et al.* 2007). Our study demonstrates that they can increase reef resilience where previously-identified features of size, age and compliance are met (Edgar *et al.* 2014). In the case of the GBR, our findings suggest that MPAs helped slow the recent decline in coral cover (De'Ath *et al.* 2012), and that overall GBR reef health would have been bleaker without this protection. Therefore, our results also reinforce the argument that MPAs should be widely supported as a means of maintaining the integrity of coral reefs in jurisdictions with the capacity to implement and enforce them. For areas where MPAs are not socially or politically tenable, alternative restrictions on gear, access and catch can support key ecosystem functions and may provide locally acceptable alternatives (McClanahan *et al.* 2012b; MacNeil *et al.* 2015). By understanding the pathways through which MPAs increase reef resilience, alternative fishing restrictions can be directed to species with the greatest ecosystem benefit, improving the portfolio of options available for coral reef management globally.

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STATEMENT OF AUTHORSHIP

CM, MAM and MJC conceived the ideas; AJC, MJE and many others collected the data; CM and MAM analysed the data; AJC and MJE helped with result interpretation; CM led the writing of the manuscript; MAM and MJC helped in drafting the manuscript, with input from all authors.

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Additional Supporting Information may be found online in the supporting information tab for this article:

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