Water quality mediated resilience on the Great Barrier Reef

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Threats from climate change and other human pressures have led to widespread concern for the future of Australia's Great Barrier Reef (GBR)[1], where increasingly frequent and severe coral bleaching, fishing, and ongoing pollution are undermining long-term persistence of coral-dominated reefs[2,3]. Future resilience of coral-dominated reefs within the GBR will be determined by their ability to resist disturbances and to recover from coral loss, generating intense interest in management actions that can moderate these processes[4–7]. Here we quantify the effect of environmental and human drivers on the resistance and recovery of hard corals to multiple disturbances within the southern and central GBR. Using a composite index for water quality, we find that reefs exposed to poor water quality recover from disturbance more slowly and are more susceptible to outbreaks of crown-of-thorns starfish and coral disease while also being more resistant to coral bleaching. Protection from fishing and increased herbivory were not associated with substantially faster recovery from disturbance. Water quality mediation of a tradeoff between resistance and recovery illustrates that, while reefs in waters of chronically-poor quality contain corals with greater bleaching resistance, there is a net negative impact on recovery and long-term hard coral cover. Given these conditions, we find that 11-23% improvements in water quality will be necessary to bring recovery rates in line with projected increases in coral bleaching among contemporary inshore and mid-shelf reefs. However such reductions are unlikely to buffer projected bleaching effects among outer-shelf

GBR reefs dominated by fast growing, thermally sensitive corals, demonstrating practical limits to local management of the GBR against the effects of global warming.

The Great Barrier Reef (GBR) has experienced unprecedented losses of hard coral cover [8]. Most coral loss on the GBR has been due to acute disturbances including storms[9,10], disease [11], outbreaks of crown-of-thorns starfish *Acanthaster* spp. (CoTS)[9], and coral bleaching [8]. Many of these impacts are predicted to become more frequent or intense due to climate change [2,10,12–14]. Key to long-term coral-dominance on reefs is whether coral communities can resist coral loss and recover sufficiently quickly between successive disturbances to be resilient and sustain viable populations[15]. However, there are currently few process-based models for quantifying intrinsic rates of increase that accurately characterize recovery. Some of the key drivers thought to influence coral cover recovery include rates of herbivory[16], coral community composition[17,18], water quality[19–22], and protection from fishing[23]. While research into individual drivers is well developed, how cumulative stressors may interact under climate change is not; the potential for non-linear responses to novel ecosystem states creates considerable uncertainty in predicting future coral reef states[24].

A key question facing many reefs world-wide is the nature of the relationship between long-term anthropogenic pollution loads and the resilience of coral reefs, which underpins millions of dollars in public and private remediation investment [25]. Changes in water quality, such as increases in dissolved nutrients and fine sediment associated with changes in land use have been linked to increases in algal densities[26], changes in coral community composition[21], and outbreaks of coral predators[27] and disease[28]. Yet despite experimental[29] and observational evidence[30], the potentially widespread role of deteriorating water quality in specifically regulating reef recovery rates is not well known. Setting targets for specific water quality parameters such as sediments and nutrient loads need to be appropriate to meet ecologically relevant targets that support ecosystem objectives and untangle the effects of multiple sources of disturbance from associated environmental and management drivers of reef resilience[31].

To quantify the effects of varying disturbance and ecosystem properties on coral reef resilience, we developed a Gompertz-based Bayesian hierarchical model for spatial coverage of hard coral cover [32] within the central and southern sectors of world's largest coral reef ecosystem, Australia's GBR. Defining resilience as the sum of resistance (ability to limit coral loss due to acute disturbance) and recovery (rate at which coral returns to pre-disturbance levels)[33], we used surveys of coral cover from 46 reefs between 1995 and 2017, that use replicate fixed-transects particularly suited to quantifying localized and long-term coral cover dynamics[34]. Importantly, during the time period under study, these reefs have been influenced by a number of major disturbances[11], including tropical cyclones[10], CoTS outbreaks[35], coral diseases[28], and severe bleaching[8]. These disturbances reduced coral cover by varying degrees, while subsequent monitoring has captured reef recovery[36]. Within four characteristic community types[37] (Extended

Data Fig 1) we quantified four key properties thought to influence resistance and recovery: protection from fisheries, coral community composition, herbivore density, and water quality. Herbivore density and coral community composition were estimated directly from the monitoring data, while fisheries protection (both no-take or no-entry) was defined by the Great Barrier Reef Marine Park Zoning Plan[38]. Water quality was defined as a metric that encompassed several water quality issues including fine sediment associated turbidity and high nutrient waters supporting high phytoplankton biomass measured as chlorophyll typically associated with the input and extent of river plumes in the wet season. The "water quality" metric is captured as the average frequency of exposure to river-influenced plumes (PF_C), which includes the average frequency of highly turbid (primary), high chlorophyll-a (secondary), and colored dissolved organic matter (tertiary) water masses[39] (see Supplemental Methods). As such, PFc represents an assessment of reduced water quality conditions in the wet season. Our approach is unique in explicitly representing potential effects of a range of conditions on the recovery rate of corals within a mechanistic population model. Thus, with a strong set of concurrent empirical data, we were able to model the resilience history of a large portion of GBR and estimate how it can be expected to respond to increasingly frequent thermal stress.

In 1995 and 2017, average coral cover was comparable (from 28% to 29%), with substantial periods of decline and recovery (Fig 1) including expected average coral cover levels between 18% and 56% (Figs 1b, 2b). Among known disturbances at locations with long term monitoring (*see* Extended Data), storms had the largest impact on coral cover (-0.22 [-1.84, 1.65]; posterior median and 95% highest posterior density interval for standardized effect sizes) followed by CoTS (-0.20 [-0.55, 0.08]), bleaching (-0.10 [-0.12, -0.08]), and coral disease (-0.02 [-0.03, -0.0]), with evidence of more intense storm impacts along the outer shelf, and greater hard coral losses from CoTS among Poritidae/Alcyoniidae and *Acropora*-dominated reefs (Fig 2e). Resistance to disturbance was also adversely impacted by increasing exposure to the riverine plume waters, measured by an increasing PF_C value and associated with greater hard coral loss from both CoTS and disease (Fig 2f), strongly supporting the assumed role of elevated nutrients increasing both CoTS larval survival[27,41] and disease prevalence[21,42].

In addition to these adverse impacts of exposure to high nutrient, high turbidity riverine flood plumes, we also found that the frequency of exposure to river-influenced plumes has led to increased coral resistance during thermal stress and bleaching events among inshore reefs. Although bleaching on the GBR typically occurs during doldrum conditions when sediment particles are likely to settle, high turbidity waters associated with riverine plume waters reduce exposure to light stress and hence the probability of a bleaching response where corals expel their algal symbionts[43]. In addition, the extreme environmental conditions characteristic of inshore settings (*e.g.* chronic runoff exposure, fluctuating turbidity, light, and temperatures) have shifted coral community composition at some locations toward more disturbance-tolerant species[44], allowing these communities to tolerate thermal anomalies better than those in the more stable thermal conditions of offshore reefs[45,46]. This increased resistance to bleaching appears to offset some of the obvious negative impacts from elevated nutrient concentrations delivered in riverine plume waters[47,48], although these effects are likely overwhelmed by the most extreme warming conditions such as those observed in 2016/2017. The major coral bleaching and mortality event in 2015-2016 and 2016-2017 severely impacted reefs world-wide[2,8], with extensive losses of hard coral that transformed coral reef assemblages across the northern (2015-2016) and central (2016-2017) Great Barrier Reef[1]. Readers may therefore be surprised that coral bleaching did not feature as the most prominent source of disturbance in our analysis. However this bleaching event was unique in the recorded history of the GBR in that it occurred primarily in the northernmost sector, long considered the 'pristine' end of the reef[1] and where limited long-term monitoring data exists.

Following disturbance, we found that coral recovery was most rapid among the *Acropora*-dominated reefs that span the outer shelf (Fig 2a), where the per-unit-cover rate of increase (hereafter recovery rate) among tabulate *Acropora* reefs (1.48 [1.36, 1.88]) was 30% to 41% higher than on soft-coral dominated reefs (1.05 [0.97, 1.30]), mixed coral assemblage reefs (1.08 [0.97, 1.43]), and Poritidae/Alcyoniidae reefs (1.13 [1.01, 1.44]) in periods with no acute disturbance (Fig 2a). This combined high intrinsic rate of increase and low density dependence (Fig 2d) underlies the rapid recovery observed among *Acropora*-dominated reefs throughout the Indo-Pacific[15,49,50]. Most striking however, was clear evidence of the strong, negative impact that exposure to high nutrient and/or the high turbidity conditions associated with riverine plume waters has on coral recovery rates across the GBR (Fig 2g), having a far greater influence than protection from fishing, likely due, in part, to the relatively low levels of fishing pressure among most GBR reefs[51].

To understand the historical impact deleterious conditions associated with high sediment and nutrient loads associated with riverine plume waters has had on hard coral recovery, we estimated maximum potential reductions in PFc that could be achieved given a theoretical return to pre-European conditions (a 65% reduction in PFc), using the average estimated proportions of anthropogenic contributions for dissolved inorganic nitrogen (DIN) and fine sediments from across the GBR[52] (Extended Data Methods). Given these theoretical levels, we find that chronic river-influenced plumes from anthropogenic influenced riverine loads have reduced recovery rates among inshore Mixed and Poritidae/Alcyoniidae reefs and mid-shelf reefs by -12% [-14%, -10%] to -27% [-31%, -21%] (Supplemental Information). Given that the riverine plume metric (PFc) represents the frequency of plume waters over a 14 year period during wet season conditions (Nov to April), the modelling of a reduction in PFc, represents one of the first broad-scale estimate of the impact coastal agriculture and development has had on coral recovery on the GBR. These negative effects are likely due to factors such as light attenuation from resuspension of fine sediment imported to the GBR via flood plumes causing reductions in coral growth[40,53,54] and symbiont photosynthesis[55], as well as from higher competition with algae that benefit from nutrient enrichment[19] limiting coral recruitment[56].

Given that water quality is the strongest management-related predictor of both reef resistance and recovery, we assessed what reduction of riverine-plume frequency (measured as PFc) would be necessary to counteract expected increases in thermal stress relative to 1995-2017 conditions. We simulated future hard coral dynamics out to 2050 from our model given projected increases in thermal stress and bleaching potential under RCP 4.5[13], now considered the most likely scenario for future climate[57], as well as GBR-specific trends[58] and the most recent empirical rates of observed thermal stress and bleaching[2] (Fig 3a). We find that, unless corals are able to rapidly adapt to warming conditions, 11% to 23% improvements in the frequency of elevated sediments and/or high wet-season nutrient plumes waters will be necessary to counteract future thermal stress expected by 2050 among inshore and mid-shelf reefs, which are exposed to the greatest PFc levels (Fig 3b,d). While plumes themselves are not anthropogenic, high PFc values do represent high frequency of brown or green waters that predominate in anthropogenic conditions. These large-scale water quality improvements are within the scope of proposed targets for sediment and nutrient loads under the State of Queensland’s Draft Reef 2050 Water Quality Improvement Plan 2017-2022[59]. However, given that the targets are not likely to be met (SCS 2017) and even with the positive effects of reduced probabilities of CoTS outbreaks accounted for in our model, current water-quality management is unlikely to buffer projected thermal stress among more intact *Acropora*-dominated reefs, due to the low exposure of offshore waters to land runoff and to resuspended sediment (Extended Data Fig 6). Given current trends[2,58], we find that more than 65% reductions in PF_C would be needed to counteract predicted bleaching rates to 2050 among offshore *Acropora* reefs, levels that exceed the change since pre-European conditions, making such an improvement likely impossible. The prospects for corals are much better if they are able to adaptively respond to recent thermal stress through natural or assisted evolution[60]. Under 80-year rolling climatology adaptation conditions[13], only modest (<5%) PF_C improvements would be expected to close the predicted bleaching gap in all but the *Acropora*-dominated reefs (Fig 3c).

Our results help to clarify the role catchment management actions could play in promoting reef resilience where high nutrients, high productivity and high turbidity changes in the inshore reefs dominates over fishing as the most pervasive driver of reef dynamics. Specifically, we find evidence that closed areas and herbivory have less influence than particular aspects of water quality (i.e turbidity) on coral recovery rates across the GBR (Fig 2g). In locations where fishing pressure is greater than the GBR, herbivory and protected areas can have a greater role in resilience-based management of reefs[6]. Even on the GBR, protected areas have been shown to increase resistance to disturbance, helping retain overall community structure[61] that will become increasingly important as climate stress increases. Our results do highlight the need to understand the influence of water quality, particularly the differences between fine sediments and high nutrients conditions on coral reef resilience more broadly, especially as it is one of the most poorly quantified and understood stressors on reefs. It is likely that improvements in different aspects of water quality is a more common driver of reef resilience in other locations, as shown in some case studies[62,63].

While local actions to mitigate climate-change impacts are unlikely to keep up with escalating threats from climate change itself [64], concurrent actions are needed to support coral reef resilience through the medium term if reefs are to have the largest opportunity to recover [65–67]. Recent back-to-back bleaching events across two thirds of the GBR underscore the need to act quickly and implement management measures that mitigate the multiple pressures facing the GBR[8]. Our results also show how mitigation of the inputs of high sediment and nutrient loads to improve water quality plume conditions along the Queensland coast will give the GBR the best possible chance to maintain some level of resilience in an increasingly disturbed future.

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Supplementary Information is available in the online version of the paper.

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Author Contributions M.A.M conceived of the study with N.A.J.G.; M.A.M., C.M., N.H.W., M.D. and S.M. collected or collated the data; M.A.M, C.M., C.D., and K.M. developed and implemented the analyses with ideas from T.R.M., S.M., and N.H.W.; M.A.M., C.M., and

N.A.J.G. wrote the paper, and all authors contributed significantly to the interpretation and editing of the manuscript.

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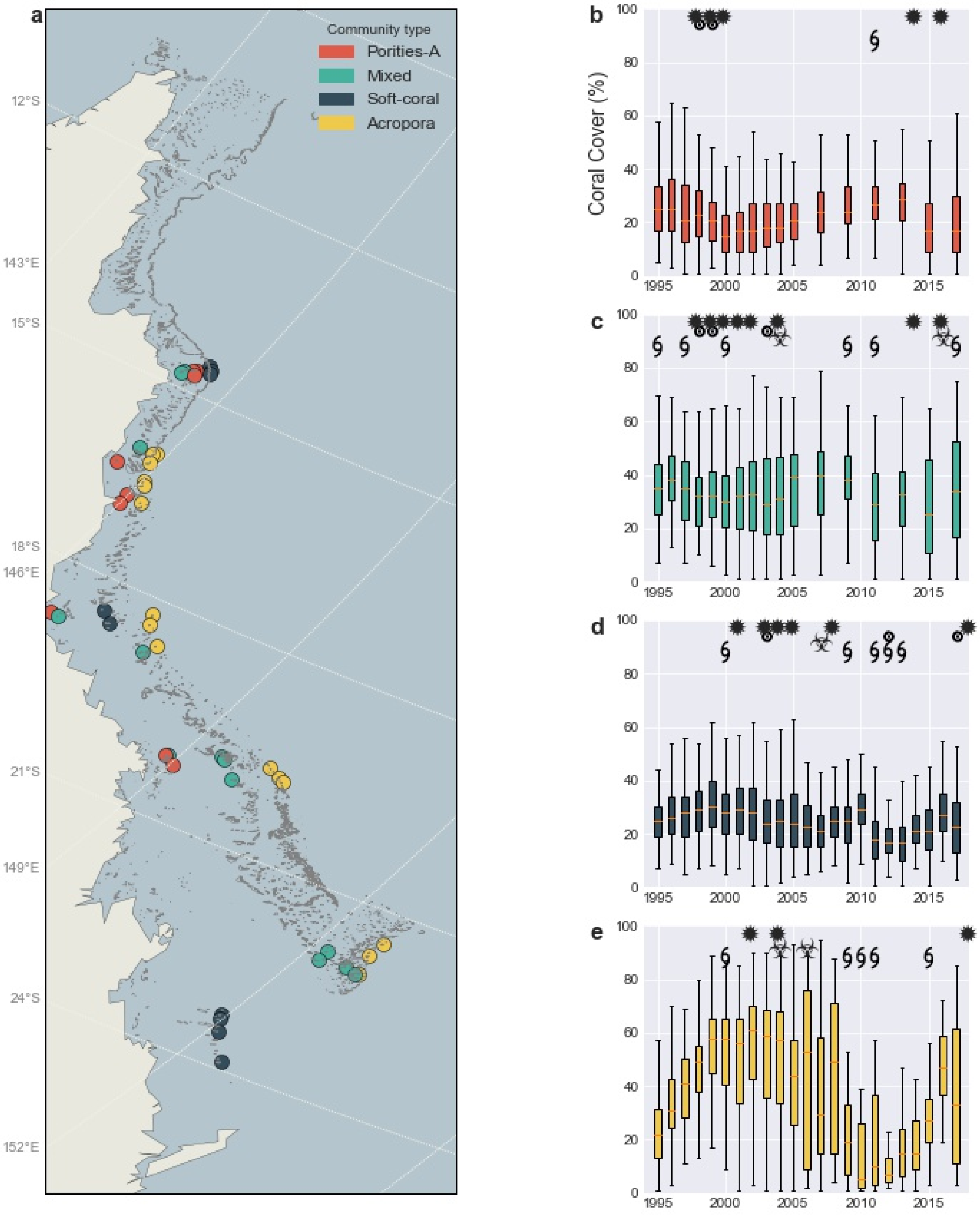

Figure 1 | Study locations and trends in hard coral cover across the Great Barrier Reef. a) Survey locations for AIMS long-term monitoring program (LTMP) reefs (n=46), 1995-2017 (n=12,523 individual transects), grouped by community type from Emslie *et al*. 2010. Trends in hard coral cover, with symbols indicating occasions when these community types were exposed to major disturbances, such as storms (§), bleaching events (☒, disease outbreaks (☣), and crown-of-thorns starfish outbreaks (✷) per year for reefs within b) Poritidae/Alcyoniidae, c) mixed, d) soft-coral dominated, and e) *Acropora*-dominated community types. Boxplots show center line (median), box limits (upper and lower quartiles) whiskers (1.5x interquartile range).

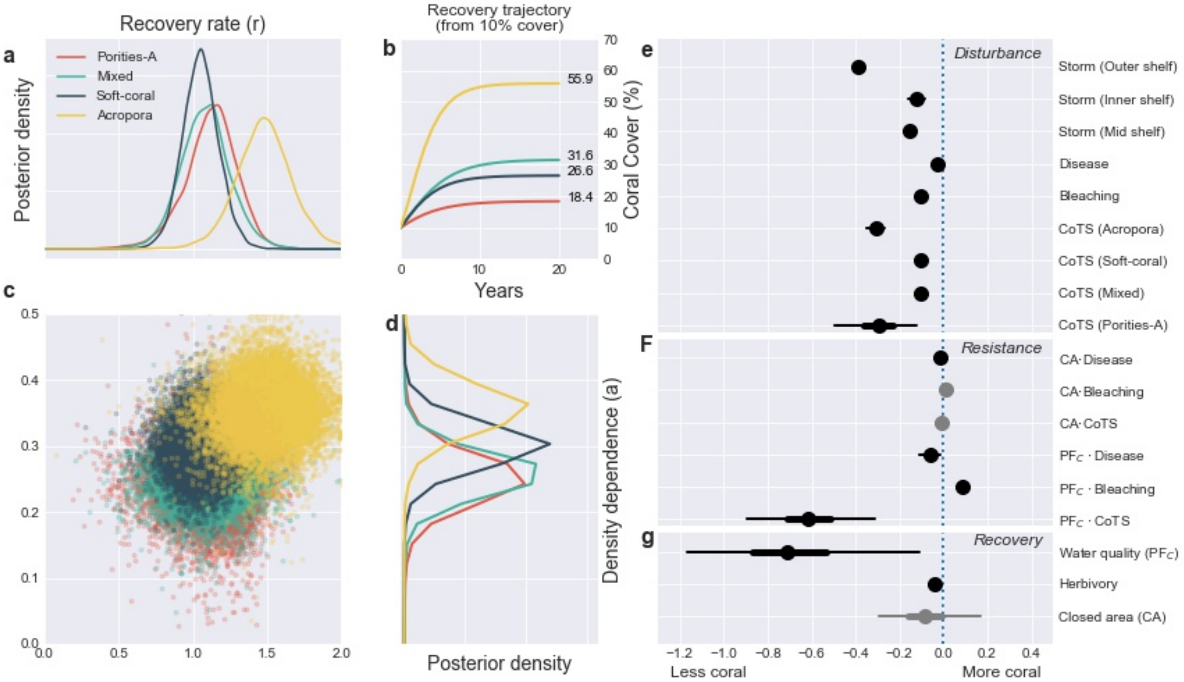

Figure 2 | Bayesian posterior model results for hierarchical model of hard coral decline and recovery across the Great Barrier Reef. Data from AIMS long-term monitoring program (LTMP) reefs (n=46), 1995-2017 (n=12,523 individual transects). a) Posterior distribution of intrinsic rate of increase (*r*) among GBR coral community types; b) median predicted recovery trajectories from 10% initial cover for GBR coral community types, given average conditions and an absence of coral loss from disturbance; c) scatterplot of joint posterior samples for model *r* (intrinsic rate of increase) and *a* (density dependence) Gompertz-based coral model parameters; d) posterior distribution of *a* among GBR coral community types; and e) posterior effect size plot for Gompertz-based coral model covariate parameters, including posterior medians (circle), 50% uncertainty intervals (thick line), and 95% uncertainty intervals (thin line), with grey dots indicating parameters where the 95% UI overlaps zero, and black dots where they do not. CA·xxx and PFc·xxx indicate interactions in the model. Full model posteriors are presented in Extended Data Figs 2 and 3.

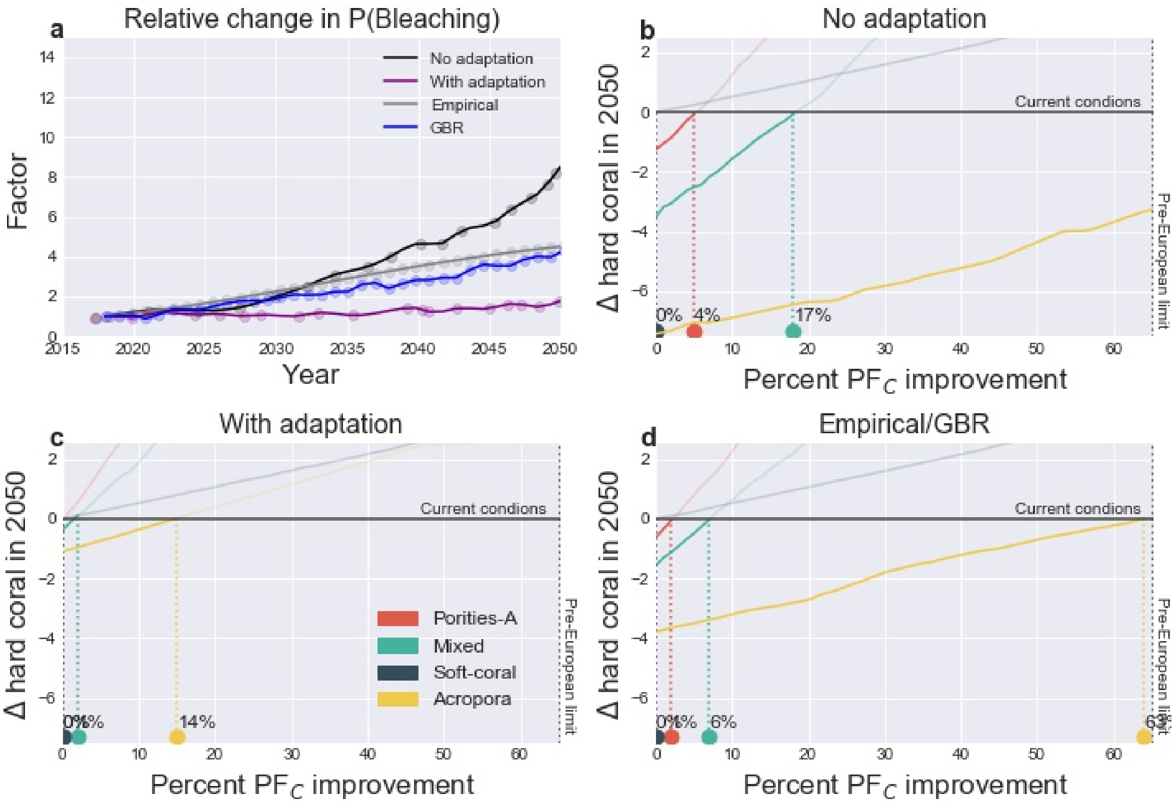

Figure 3 | Projected effects of changes in the average frequency of river-influenced plumes across the Great Barrier Reef. a) Increases in relative bleaching potential under RCP 4.5 given no adaptation, with a rolling 80 year window of adaptation[13], expected GBR-specific trend from van Hooidonk et al. 2016, and the empirical trend estimated from Hughes et al. 2018. Projected net percent differences in median hard coral cover (Δ) relative to long-term expected coral cover under current disturbance conditions (i.e. no increase in frequency of bleaching-derived coral loss) given improvements in average river influenced plumes (PF_C) given b) no adaptation, c) with adaptation, and d) average trends from two published estimates[2,58]. Points along the x-axis indicate level of PF_C improvement necessary to counteract projected coral loss due to increases in the frequency of destructive bleaching in panel A. Pre-European limits (dotted line on far right) derived from estimates of proportion of anthropogenic influence.

METHODS

Survey data

The data underlying our analysis come from the Australian Institute of Marine Science (AIMS) Long Term Monitoring Program (LTMP)[68] which includes 46 reefs that were monitored annually between 1993 and 2005, and biennially thereafter. Our data includes surveys from 1995 to 2017 (conducted October to April each year), with multiple bleaching and other disturbance events. Note that the most severe bleaching events of 2016/2017 occurred north of most survey locations, where no long-term monitoring exists and our data and model do not include samples from the northernmost sector or the heavily-impacted Keppels region. Surveyed reefs were primarily in the central and southern GBR, the areas where routine monitoring occurs (Figure 1a). Importantly for this study, each of the 46 survey reefs includes 15 fixed-position 50 m transects, a survey design ideally suited to studying inter-annual dynamics. Within each survey reef, five transects were spaced <50 m apart at each of three sites along the 6-9m contour of the reef slope. For each transect in each observed year, the percentage of hard coral cover was estimated by the percentage of 200 randomly selected individual points, five at a time, from each of 40 still images of the benthos and identifying to the genus level [69].

2016/2017 Bleaching event

Because quantifying reef dynamics requires long-term monitoring data that includes a range of disturbance events and subsequent periods of recovery, these northernmost locations currently provide little information as to rates of recovery. They will do so however over the coming decades where – bar an additional severe bleaching event – their recovery will provide a test of our estimated recovery rates absent human influence. Therefore, from our model we predict there is a greater than 50% chance that *Acropora*-dominated reefs within the northernmost sector of the GBR will reach 60% [38%, 91%] average coral cover within 10 years (from 10% median coral cover[1]). These predictions are into areas north of our study area and constitute an important test of the applicability of our approach among reefs outside our survey data.

Use of the term 'resilience'

Our definition of resilience specifically refers to the factors that moderate the impact of acute disturbances (resistance) and the rate at which corals increase after experiencing them (recovery). While we recognise a more nuanced, alternative definition of resilience as being "the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks" [70], our study does not compare structure and function of coral reefs explicitly. Rather our goal was to quantify hard coral cover dynamics through time, and to understand the various processes that influence them. In this, our formulation is clear and fit for purpose.

Model covariates

To make inferences regarding potential factors influencing coral decline and recovery, we collected covariates purported to impact these processes, including levels of herbivory, water quality, fisheries restriction, coral community type, and disturbance history. While some covariates were unambiguous (such as zoning), for most processes we selected the best-available covariates that captured their key features. At the scale of our analysis, this process necessarily averages over factors not represented within these covariates, which is common in statistical modelling but also makes our results conditional on the assumptions made in using these covariates and the structure of our model. It is important to note that we standardized each model covariate so as to be broadly comparable within resilience and recovery model sub-components. This means that when we state 'given average environmental conditions' about a given effect size for a covariate, it assumes the other covariates are at their standardized average (0), which will often not occur in practice. This formulation allows us to most readily compare among groups and assess the relative importance of model covariates. Sub-headings include abbreviations used in the model equations below.

Coral community type - CCT

For each transect in each observed year, the percentage of hard coral cover was estimated by randomly selecting 200 individual points, five at a time, from each of 40 still images of the benthos [69]. Our communities followed Emslie *et al.* 2010[37], who used a principal components analysis (PCA) of average proportions of identified coral families to allocate each of the survey reefs to one of four coral community types, including Acropora, Poritidae/Alcyoniidae, mixed-coral, and soft-coral dominated reef types (Figure S1). These community types formed the basis of hierarchical community groupings for subsequent modelling, where individual reefs were nested within specific community types.

Disturbance history – COT, STO, BLE, DIS, UNK

While conducting LTMP surveys, AIMS staff recorded instances where >5% of total hard coral cover was lost between surveys, assigning attribution to the loss based on five potential disturbances: crown-of-thorns starfish outbreaks (COTS); storms or cyclones (STO); coral bleaching (BLE); coral disease (DIS); or, where the cause of coral loss was not identified, unknown (UNK). Each disturbance was identified by distinctive and identifiable effects on corals, such as the presence of CoTS individuals or feeding scars, or dislodged and broken coral indicative of cyclone damage[71]. Each of these disturbances was originally coded for presence (1) or absence (0) per transect per year, which we matched to existing quantitative estimates of disturbance severity for subsequent modelling. Specifically, percent coral cover bleached was interpolated using inverse distance weighting (maximum distance = 1°; minimum observations = 3) from extensive aerial surveys for the three mass bleaching events on the GBR (1998, 2002, and 2016/2017). Interpolated maps of CoTS densities were generated by inverse distance weighting (maximum distance = 1°; minimum observations = 3) from the manta tow data collected by the Australian Institute of Marine Science in every year between 1996 and 2017 [72]. The potential for cyclone damage was estimated based on 4-km resolution reconstructed sea state as per Puotinen et al. 2016 [73]. This model predicts the incidence of seas rough enough to severely damage corals (top one-third of wave heights >4m) caused by cyclones for every cyclone between 1996-2017. CoTS and bleaching are sometimes thought of as ecosystem responses to disturbances from nutrients and thermal stress[35]. Note we did not plot UNK effects in the text because these represent losses of corals that didn't have attribution in the data, but are likely from one of the other recorded categories and therefore constitute observation error.

Herbivory - HRB

To represent the potential influence of herbivorous fish on the disturbance and recovery dynamics of coral reefs [74] we included a measure of the total abundance of herbivorous reef fishes present in each survey year. As part of the LTMP, AIMS staff have also collected concurrent reef fish data, using standardized belt transect methods [68]. For each of the LTMP transects, divers conducted underwater visual surveys (UVC) whereby they estimated the abundance of herbivorous fishes (including scrapers, excavators, grazer/detritivores, and algal browsers)[75] present within 2.5m either side of a 50 m tape measure used to demarcate the survey area.

Zoning – MPA

To account for potential impacts of fishing on the disturbance and recovery dynamics of the LTMP survey reefs, we included a dummy variable to indicate if fishing was present (0) or not (1). Thirty-five percent of reefs within the GBR have been protected as no-fishing or no-entry zones since at least 2004, including many within the LTMP (Table S1); we included both no-fishing and no-entry areas in our MPA covariate. It is worth noting that there is some evidence of poaching affecting ecosystem function among no-fishing reefs on the GBR[76].

Water quality exposure – PF_C

In the GBR region, the use of MODIS true colour imagery has provided a spatially rich technique in the estimation of river plume extent and improved the assessment of the level of exposure of inshore coral reefs and seagrass meadows to river plumes. River plume mapping utilising true colour imagery has been applied as a method of characterising the water quality conditions associated with periods of elevated river flow through the wet season. Various products have been produced using different methods of extraction, aggregation through annual and multi-annual time frames, and integration to provide robust information on annual wet season conditions and to report decadal time frames around water quality during wet season conditions. While PFc represents an assessment of reduced water quality conditions in the wet season, future work should consider the complexity of the year round turbidity issues associated with the resuspension of the finer sediment during high wind conditions[31,40]

River plume maps are produced using MODIS Level-0 data acquired from the NASA Ocean Colour website (http://oceancolor.gsfc.nasa.gov) and converted into true-colour images with a spatial resolution of 500 m × 500 m using SeaDAS [77]. The true colour images were then spectrally enhanced from Red-Green-Blue to Hue-Saturation-Intensity colour systems and classified to six distinct river plumes water types defined by their colour (RGB/HSI signatures) properties and hereafter referred to as plume colour classes [39,78]. Three types of plume waters were distinguished following previously described methods[79,80] as: *Primary*, characterized by high turbidity and nutrients; *secondary*, characterized by high chlorophyll; and *tertiary*, characterized by high color dissolved organic material (CDOM). The clustering of the colour classes into six groups characterising the water types in the river plumes is through supervised classification using spectral signatures from the changes in colour associated with the gradient of river plumes. Each of the defined six colour classes (CC1–CC6) is characterised by different concentrations of optically active components (TSS, CDOM, and chlorophyll-a) that influence the light attenuation and can vary the impact on the underlying ecological systems. CC1–CC3 correspond to the brownish turbid water masses with high sediment and CDOM concentrations, CC4 and CC5 to the greener water masses with lower sediment concentrations favouring increased coastal productivity, and CC6 is the transitional water mass between plume waters and marine waters[39,54]. These categorizations were used to underpin our composite index, PF_C which represents the frequency of all plume water types (i.e CC1 – CC6). Thus, the PFc is a metric that represents a range of water quality conditions, high turbidity, high CDOM and increased productivity.

Frequency of riverine plume exposure for each reef was measured using the MODIS satellite observations from 2000 – 2014. Data represent the proportion of wet season weeks, defined as the period from November to April (N = 22 weeks per year) in which plumes, corresponding to the defined colour classes (CC1 – CC6) were present. To avoid backscattering interference leading to false plume characterization at or near reef margins, plume data were processed as follows[66]: Firstly, the Great Barrier Reef Marine Park Authority reef polygon layer, with a 1 km buffer applied, was used to eliminate any plume data pixels it intersected. Secondly, the remaining valid pixels were used to interpolate plume data across the data gaps (reef locations) resulting from the first step. The resulting clean layer was used here to assess reef exposure to the plume frequency (PFc).

Coral dynamics model

Our lack of overall change in coral cover estimates differed from previously-reported losses of total cover on the GBR – which were from 28% to 22% [34] and from 28.0% to 13.8% [9] - reflecting methodological, spatial, and temporal differences among datasets and the problems inherent in using linear trends to describe long-term, density-dependent dynamics. To overcome these issues, we employed a Gompertz-based modelling approach to estimate recovery rates independent of the magnitude of prior coral loss, using a hierarchical structure that included four characteristic community types: Acropora, Poritidae/Alcyoniidae, mixed-coral, and soft-coral dominated reefs [37]. Our model includes two growth components: an intrinsic growth rate and a term for density dependence that controls for slower growth rate at near carrying capacity. As the resilience of coral reefs rests on a combination of their ability to resist disturbances and to recover from them, our models included explicit representations of both processes. Our modelling approach is unusual in explicitly representing both decline and recovery using what have traditionally been population models for abundance, rather than simple linear trends. Our development of these models was based on the innovation of Fukaya et al. 2010[32], who reconciled Gompertz-based population models with coverage-limited sessile organisms. A similar approach has been used previously by Osborne et al. 2017[81], based on our initial development of these methods for this analysis. To model resistance to disturbance, we include explanatory variables relating to levels of fishing protection and herbivory, as well as the interactions between disturbance types and both our index of the frequency of riverine plume waters (PF_C) and closed areas (CA). Post-disturbance recovery rates were modeled using variables relating to water quality exposure (PF_C), herbivory, and protection from fishing (CA).

To quantify the coral disturbance and recovery dynamics of LTMP reefs between 1995 and 2017, we developed a coverage-based Bayesian hierarchical statistical model based on the work of Fukaya *et al*. 2010 [32]. This Gompertz-based model quantifies the intrinsic growth rate (r) and strength of density dependence (a) for sessile species, expressed as coverage of a defined sampling area. In our case this was the number of visual points (y) out of 100 that contained hard coral within the LTMP data per transect. Using a Binomial (BIN) observation model, we assumed a hierarchy where transect level observations (*i*) at time (*t*), were nested within reef (*r*), nested within each community type (*c*):

$$y_{crt,i} \sim BIN(100, p_{crt,i}) \quad [1]$$

with mean model

$$\begin{aligned}\log(p_{crt,i} \times 100) = {} & (r_{cr} + \gamma_7 HERB_{t,i}) + (1 - a_{cr})\log(y_{crt-1,i}) + \gamma_{2,c}COT_{t,i} + \gamma_{3,c}STO_{t,i} + \gamma_{4,c}BLE_{t,i} + \gamma_{5,c}DIS_{t,i} \\ & + \gamma_{6,c}UNK_{t,i} + \gamma_8 BLE \times PF_{C,r} + \gamma_9 COT \times PF_{C,r} + \gamma_{10}DIS \times PF_{C,r} + \gamma_{11}UNK \times PF_{C,r} + \gamma_{12}BLE \\ & \times CA_r + \gamma_{13}COT \times CA_r + \gamma_{14}DIS \times CA_r + \gamma_{15}UNK \times CA_r\end{aligned}$$

and where

$$a_{cr} \sim N(a_c, \sigma_{ac})$$

$$r_{cr} \sim N(r_c + k_0 CA_r + k_1 PF_T\,,\ \sigma_{rc})$$

$$a_c, r_c, k_0, k_1, \gamma_{1\ldots15} \sim N(0, 100)$$

$$\sigma_{ac}, \sigma_{rc} \sim U(0,100)$$

Note that in this formulation, each coral community type had their own global mean at the top level of the hierarchy. These models were run in a Bayesian framework, using the PyMC3 package in Python[82], with inferences made from 5000 samples of the No U-Turn Sampler (NUTS) algorithm. Parallel chains were run, from starting values initialized automatically by an

Automatic Differentiation Variational Inference (ADVI) algorithm, to look for convergence of posterior parameter estimates using the Gelman-Rubin convergence statistic (R-hat); posterior traces and predictive intervals, as well as Bayesian p-values[83] were examined for evidence of convergence and model fit. All model diagnostics showed efficient exploration of the posterior and provided no evidence for lack of model fit (Extended Data Figs S2, S3, S4).

Disturbance probabilities

To quantify the disturbance history within the LTMP data from 1995 to 2017, we elected to model the average annual disturbance using a simple Bayesian hierarchical Bernoulli model (BNI) for each coral community type and disturbance (DIS):

$$\begin{gathered} DIS_t \sim BIN(p_{dc}) \\ p_{dc} = invlogit(\beta_{dc}) \qquad [2] \\ \beta_{dc} \sim N(0, 10) \end{gathered}$$

yielding a community-type specific disturbance probability (p_{dc}) for each disturbance type (*d*), where DIS is one of COT, STO, BLE, DIS, or UNK. Probabilities from this model were then multiplied by median disturbance severity when used in our future projections.

Pre-European conditions

To evaluate the effect of increased sediment plumes on recovery rates and the capacity to compensate for increased bleaching events, we initially relied on paleo-ecological estimates from McCullugh et al. 2003[84], who used coral cores from the central GBR to estimate modern and pre-European barium loads at $4.8+0.6\text{x}10^{12}$ and $3.5+0.2\text{x}10^{12}$ L/wk respectively (a 66% difference). However, based on the comments of a knowledgeable reviewer, we revised this threshold to better reflect contemporary understanding of anthropogenic nutrient and sediment loads. Specifically we used the average proportion of DIN and fine sediment loads attributed to anthropogenic sources among the Wet Tropics, Burdekin, Mackay/Whitsunday, Fitzroy, and Burnett Mary NRM regions in Tables 10 & 11 of Brodie *et al*. 2017[52] to estimate an overall potential *PFc* improvement of 65% (See *Figures and summary statistics* code below for exact calculations). Note however that our PFc composite index has only recently been developed over the entire GBR; the next step in this work is to calculate PFc at an individual catchment level to allow specific management actions across the GBR, in line with both the scientific consensus statement[85] and the target water quality[52] reports.

Future projections

Current conditions scenario

To estimate how future changes in overall water quality would influence the disturbance and recovery dynamics of LTMP reefs, we simulated a range of improved water quality scenarios from 2018 to 2050 by proportionally reducing each of PF_C values by 1% increments (up to a 66% reduction), while sampling from the posterior distributions of model [1] and the disturbance probabilities from [2]. These simulations were run 9999 times per PF_T value, initiated using the observed 2015 hard coral cover values.

Bleaching scenarios

The frequency of coral bleaching events is widely predicted to increase steadily over coming years [2], putting coral reefs in great danger of repeated bleaching events from which they have insufficient time to recover. To simulate realistic scenarios for increased bleaching frequency, we used modelled data from the 80 year rolling climatology scenario in Figure S1 of Logan *et al.* 2014[13] to develop a bleaching factor relative to 2017. Specifically, we scaled the predictions in that figure by the value in 2017, giving us a ratio of predicted bleaching probability per year out to 2050 (Figure 3A) that we used to re-scale the probability of bleaching per year, relative to the posteriors in model [2]. We then simulated from the posteriors of models [1] and [2], as for the current conditions scenario above, but multiplying the annual bleaching probability by the new bleaching factor ratios. In keeping with the results of Logan *et al.*[13], this process included both a no-adaptation scenario, where the bleaching probability remains constant as temperatures increase, and a rolling-window of adaptation, whereby corals are able to adapt to an 80-year window of change in the underlying climate[86]. We also included a GBR-specific estimate of relative projected bleaching probability, using the predicted increase in degree heating months

(DHM) under RCP 4.5 from van Hooidonk et al[58]. Finally, given the dramatic, large-scale bleaching events on the GBR in 2016, we downloaded the data from Hughes et al. 2018[2] and used the same linear modelling approach they did, but in a Bayesian framework, to estimate the projected trend in severe bleaching recurrence through to 2050 (See supplemental code; Extended Data Fig 5). Because this probability of severe bleaching exceeds that of actual mortality, we re-scaled the projected trend represented by the blue line in Extended Data Figure 5 relative to its value in 2017, giving an additional bleaching factor ratio based on their empirical results. As above, this bleaching factor ratio was multiplied by our estimated probability of bleaching mortality in simulating future bleaching events.

Code and data to reproduce the entire analysis is available on GitHub:

Bayesian hierarchical model:

https://gist.github.com/mamacneil/fb907d588e13c0a359fbad11359cceac

Annual disturbance probabilities:

https://gist.github.com/mamacneil/3b35088bbcc0da0957ccf89c7ba11956

Empirical model from Hughes et al. 2018:

https://gist.github.com/mamacneil/245bb4c009c0c2637772dc6fa23e37cd

Plots from Hughes et al. 2018 analysis:

https://gist.github.com/mamacneil/967430a86a195587d9dc2e97d1a91c1f

Future disturbance simulations:

https://gist.github.com/mamacneil/06f814247816c0b1254045284435b695

Figures and summary statistics:

https://gist.github.com/mamacneil/bcb49741174174960a6ecd9c93bb56eb

Data:

All code and be posted to an open GitHub repository upon publication.

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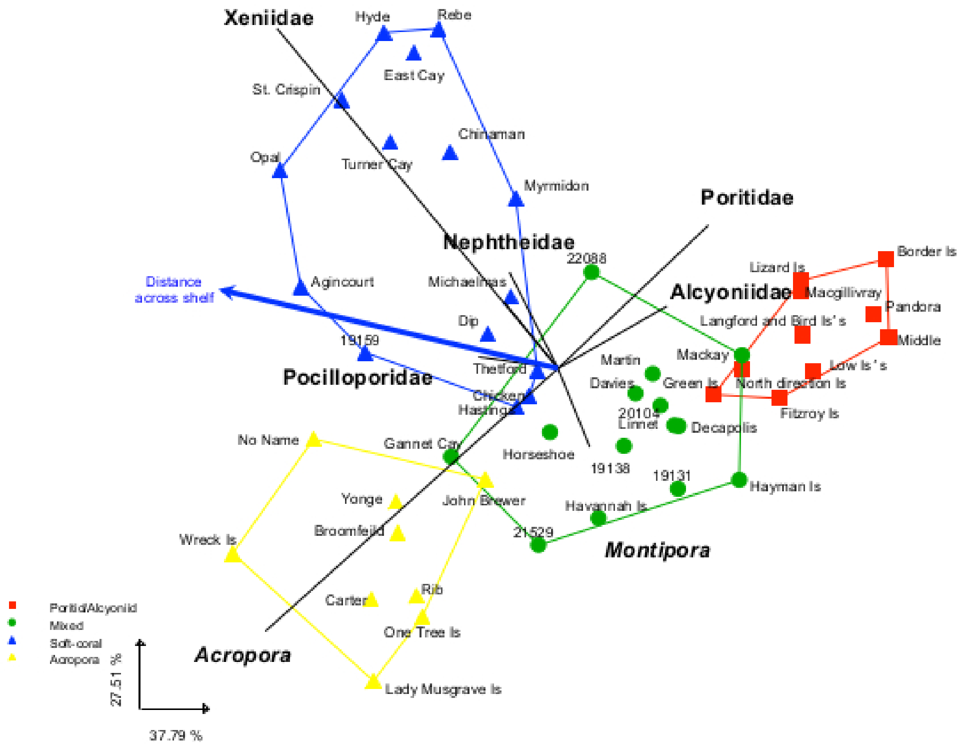
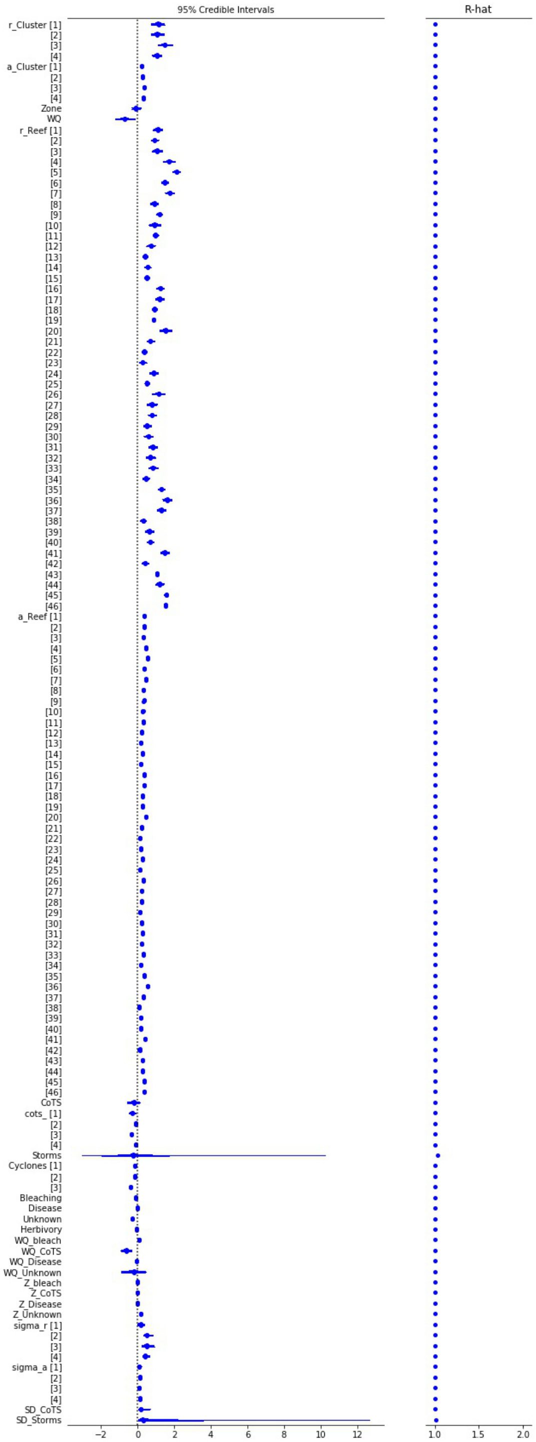
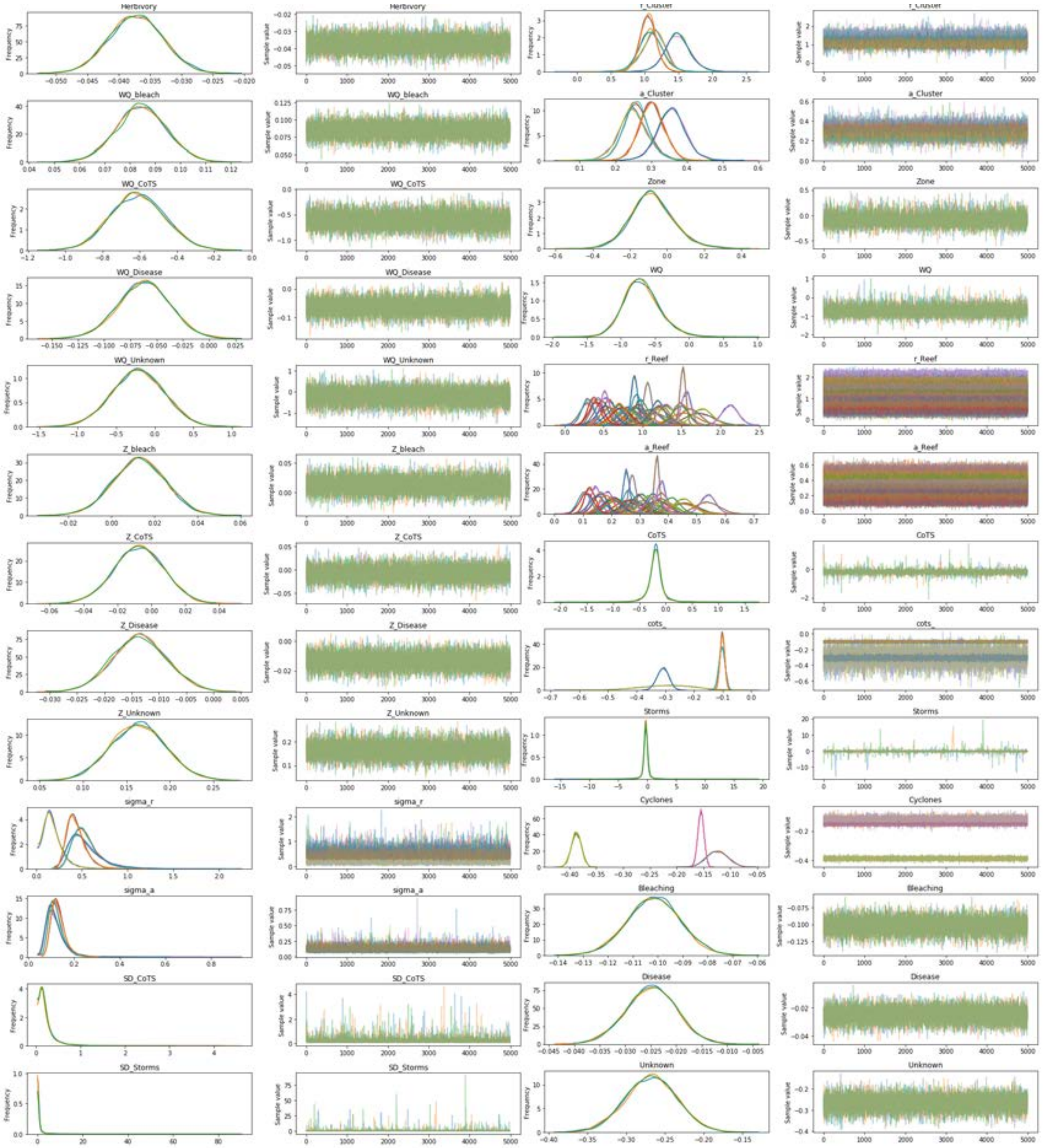


Extended Data Figure 1 | Principal component analysis clustering of benthic community composition across the Great Barrier Reef. Underlying data are from 690 transects surveyed annually on 46 reefs within the Australian Institute of Marine Science Long Term Monitoring Program 1995-2017. After Emslie *et al*. 2010[37].

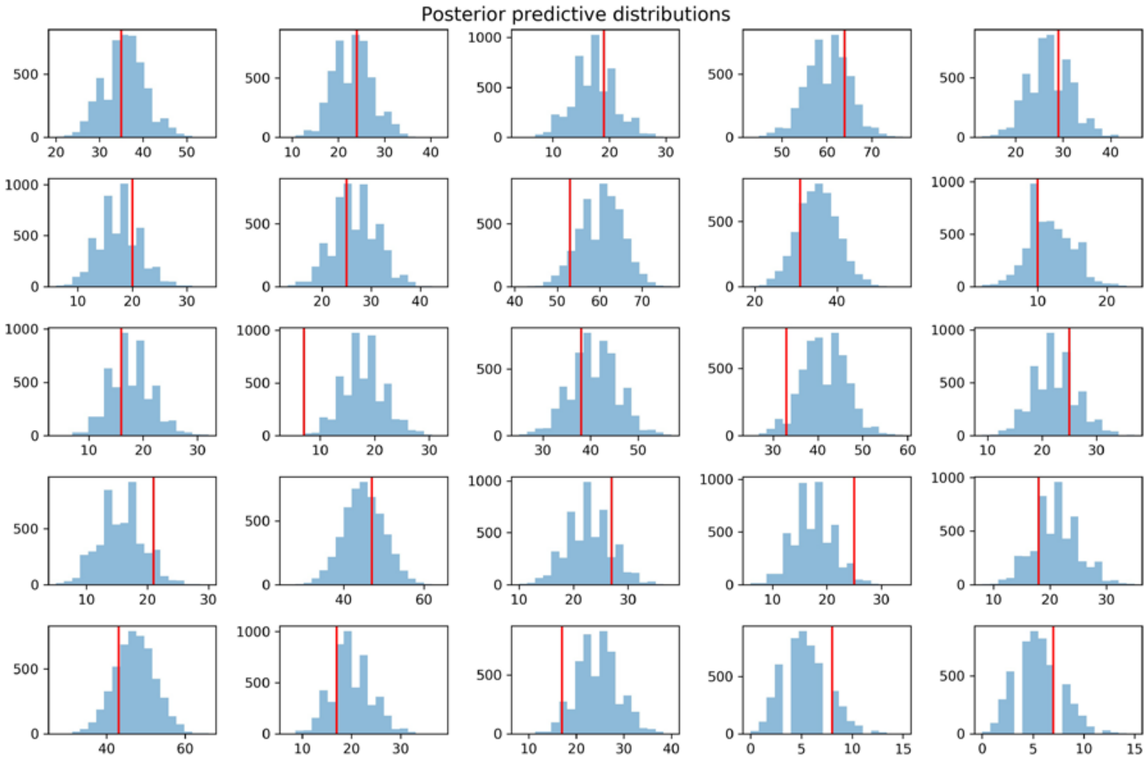


Extended Data Figure 2 | Posterior densities and trace plot of parameter estimates for a Bayesian hierarchical model of coral cover across the Great Barrier Reef. Underlying data are from 690 transects surveyed annually on

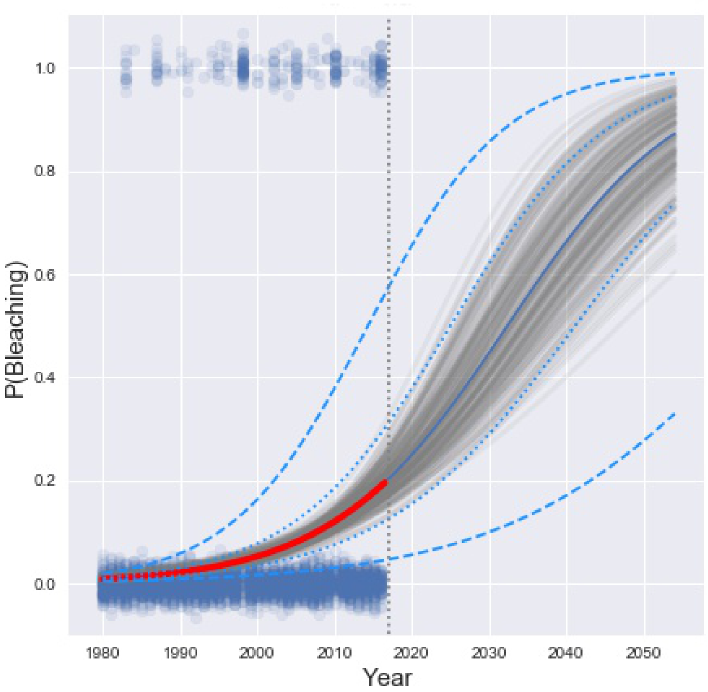
46 reefs within the Australian Institute of Marine Science Long Term Monitoring Program 1995-2017. Note the Z in the parameter names refers to closed areas (CA).



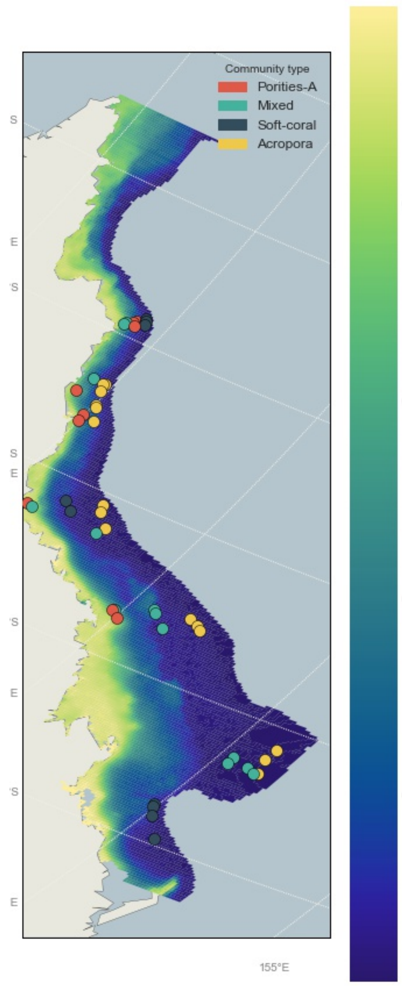
Extended Data Figure 3 | Posterior model diagnostics for a Bayesian hierarchical model of coral cover across the Great Barrier Reef. Posterior forest plot of a) parameter estimates (posterior median, 50% (thick line) and 95% (thin line) uncertainty intervals) and b) Gelman-Rubin convergence statistics (R-hat) for a coral disturbance (>5% coral loss) probabilities from 690 transects surveyed annually on 46 reefs within the Australian Institute of Marine Science Long Term Monitoring Program 1995-2017.



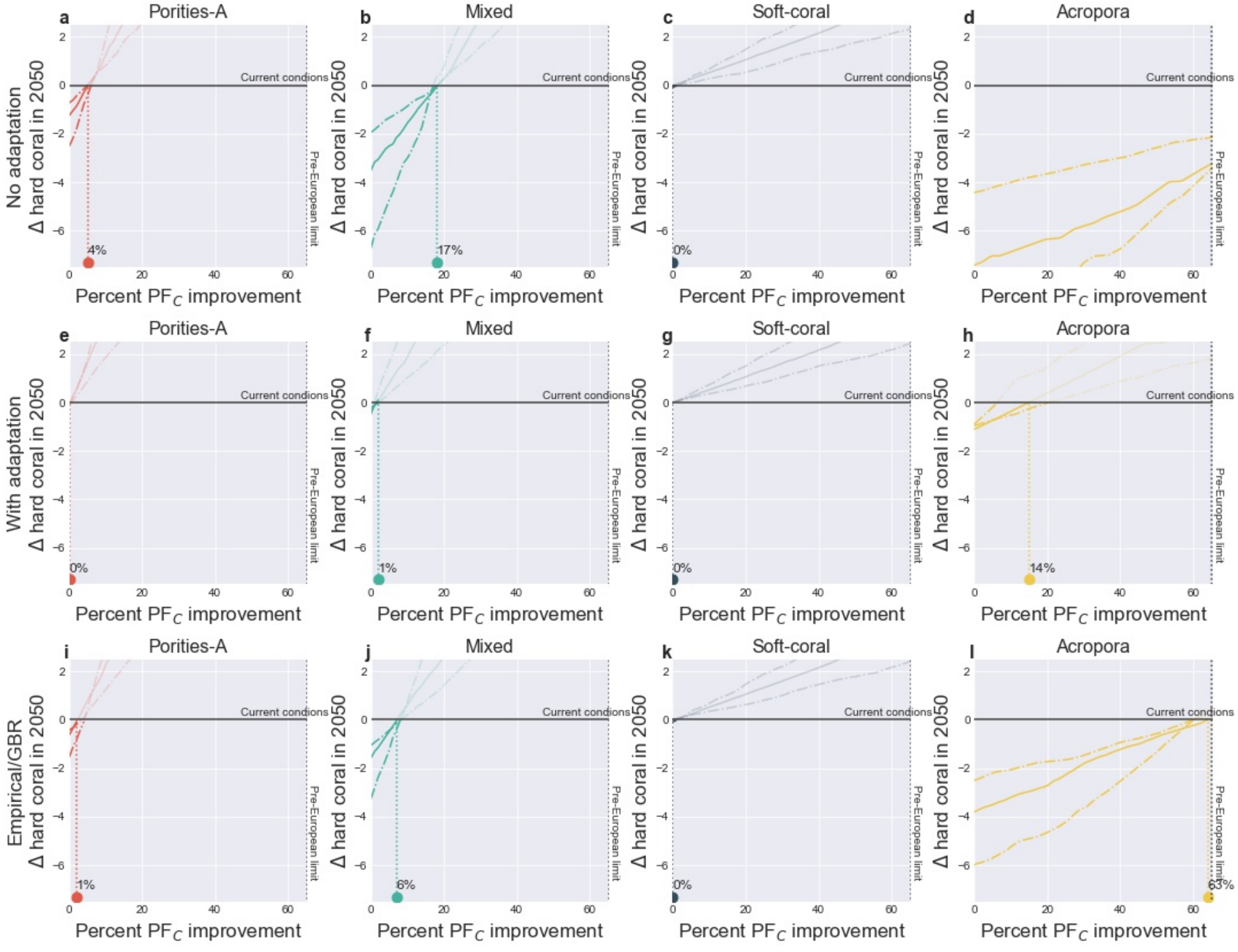
Extended Data Figure 4 | Diagnostic plots of model fit for a Bayesian hierarchical model of coral cover across the Great Barrier Reef. Posterior predictive distributions (ppd; blue) of 25 random data points (red lines) for observed hard coral cover along the Great Barrier Reef. Relative correspondence between observed data and expected distribution given similar conditions (i.e. each ppd) is representative of adequate model fit. Red lines are beyond the 95% highest posterior density of their predictive distribution are evidence of inadequate model fit for that datum. The Bayesian p-value for overall model fit was 0.56, providing no evidence of our model being inconsistent with the observed data.



Extended Data Figure 5 | Estimated relationship of severe bleaching occurrences through time. Data (blue circles) extracted directly from supplemental table S1 of Hughes et al. 2018[2], consisting of severe (S; >30% bleached) coral bleaching records from 100 fixed global locations from 1980 – 2016. Estimated trend (red line) was estimated from a Bayesian generalized linear model of occurrences through time; plot includes 50% (dotted blue lines) and 95% (dashed blue lines) uncertainty intervals for the predicted trend, as well as 100 realizations of the expected trend (grey lines) generated from the model posteriors. Solid blue trend line beyond the vertical dotted line was used as an empirically-based potential bleaching scenario in our future projections.



Extended Data Figure 6 | Derived index of average frequency of river-influenced plumes (PFc) across the Great Barrier Reef. Survey locations for AIMS long-term monitoring program (LTMP) reefs (n=46) grouped by community type from Emslie *et al*. 2010[37]. Index values are 0-1 scaled from combined primary (high turbidity and nutrients), secondary (high chlorophyll), and tertiary (high color dissolved organic material) waters, derived from MODIS true colour imagery from 2000 to 2014.



Extended Data Figure 7 | Approximate 50% uncertainty bounds for projected effects of changes in the average frequency of river-influenced plumes across the Great Barrier Reef, as represented in Figure 3. Scenarios for increases in relative bleaching potential under RCP 4.5 (rows) given no adaptation, with a rolling 80 year window of adaptation[13], and average expected GBR-specific trend from van Hooidonk et al. 2016 and the empirical trend estimated from Hughes et al. 2018. Projected net percent differences in median hard coral cover (Δ) relative to long-term expected coral cover under current disturbance conditions (i.e. no increase in frequency of bleaching-derived coral loss) given improvements in average water quality (PF_C). Points along the x-axis indicate level of PF_C improvement necessary to counteract projected coral loss due to increases in the frequency of destructive bleaching. Pre-European limits (dotted line on far right) derived from estimates of proportion of anthropogenic influence.