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Predicting climate–driven regime shifts versus rebound potential in coral reefs

Nicholas A. J. Graham[1], Simon Jennings[2,3], M. Aaron MacNeil[1,4], David Mouillot[1,5] & Shaun K. Wilson[6,7]

Climate-induced coral bleaching is among the greatest current threats to coral reefs, causing widespread loss of live coral cover[1]. Conditions under which reefs bounce back from bleaching events or shift from coral to algal dominance are unknown, making it difficult to predict and plan for differing reef responses under climate change[2]. Here we document and predict long-term reef responses to a major climate-induced coral bleaching event that caused unprecedented region-wide mortality of Indo-Pacific corals. Following loss of >90% live coral cover, 12 of 21 reefs recovered towards pre-disturbance live coral states, while nine reefs underwent regime shifts to fleshy macroalgae. Functional diversity of associated reef fish communities shifted substantially following bleaching, returning towards pre-disturbance structure on recovering reefs, while becoming progressively altered on regime shifting reefs. We identified threshold values for a range of factors that accurately predicted ecosystem response to the bleaching event. Recovery was favoured when reefs were structurally complex and in deeper water, when density of juvenile corals and herbivorous fishes was relatively high and when nutrient loads were low. Whether reefs were inside no-take marine reserves had no bearing on ecosystem trajectory. Although conditions governing regime shift or recovery dynamics were diverse, pre-disturbance quantification of simple factors such as structural complexity and water depth accurately predicted ecosystem trajectories. These findings foreshadow the likely divergent but predictable outcomes for reef ecosystems in response to climate change, thus guiding improved management and adaptation.

Some mass bleaching events have resulted in the loss of almost all live coral within individual nations[3]. Examples of coral recovery following severe bleaching have been documented[4,5], yet theory predicts that regime shifts to new benthic assemblages, such as macroalgae, are also likely[2]. To date, there are no documented coral reef regime shifts attributed specifically to climate change. Evidence for coral reef regime shifts due to other causes comes almost exclusively from the Caribbean[6,7], with limited knowledge from the more extensive and diverse Indo-Pacific reef province[8]. Ongoing uncertainty about Indo-Pacific coral reef responses to climate impacts has generated considerable debate regarding appropriate management and adaptation plans, especially those related to no-take marine reserves[9,10], that can be resolved through understanding site and ecosystem characteristics that dictate reef ecosystem trajectories.

Using a 17-year data set, spanning a major climate-induced bleaching event, we assess the long-term ecosystem dynamics of 21 reef sites across the inner islands of Seychelles. Seychelles reefs were the most severely affected globally by the 1998 coral bleaching event, in which a strong El Niño coincided with the Indian Ocean dipole[11]. Across all sites before the bleaching event, average hard coral cover was 28% and macroalgal cover 1% (Fig. 1a), within average bounds for the Indian Ocean region at the time[12]. The mass bleaching event was severe across all reefs in the inner Seychelles, with coral cover reduced by >90%[13]. Both hard coral cover and macroalgal cover steadily increased between 2005 and 2011,

with high heterogeneity reflecting markedly different trajectories among sites (Fig. 1a, Extended Data Figs 1 and 2).

Using four complimentary metrics (Methods), we defined a recovering reef as having greater post-disturbance coral cover than macroalgae cover, with coral cover remaining high or increasing. A regime shifting reef was defined as having greater post-disturbance macroalgal cover than coral cover, with macroalgal cover remaining high or increasing. We used an index, based on the Euclidian distance from pre-bleaching benthic composition, to visualize the differing benthic trajectories of
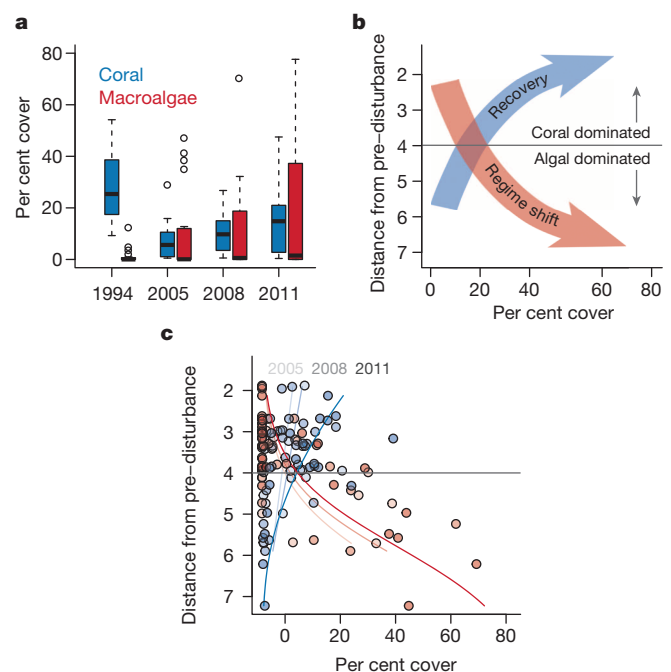

Figure 1 | Recovery and regime shift dynamics on Seychelles coral reefs. a, Box (median and 50% quantile) and whisker (95% quantile) plots of coral cover and macroalgal cover in 1994 and through time after the 1998 bleaching event ($n = 84$). **b,** Conceptual diagram for visualizing recovery and regime shift dynamics, using post-disturbance cover of coral (blue) and macroalgae (red) and Euclidian distance of benthic composition from pre-disturbance values. **c,** Recovery and regime shifts on Seychelles reefs. Lines are multinomial model fits for percent coral and macroalgae on each of the 21 reef sites (years distinguished by shading), with Euclidian distance from pre-disturbance composition as a predictor ($n = 63$). Each reef site is represented by two points, one for coral cover (blue dots) and one for macroalgal cover (red dots). Twelve reefs (top of figure) are recovering, moving towards pre-disturbance (1994) compositions, with increasing coral cover and low macroalgal cover, whereas 9 reefs are regime shifting, with increasing distance from 1994 compositions, increasing macroalgal cover and low coral cover (Extended Data Table 1, Extended Data Fig. 4).

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regime shifting and recovering reefs (Fig. 1b). Of the 21 reefs surveyed, 12 followed a post-bleaching recovery trajectory, with live coral cover increasing through time to an average cover of 23% by 2011, macroalgal cover remaining low (<1%), and benthic composition moving towards that observed in 1994 (Fig. 1c, Extended Data Table 1, Extended Data Figs 3 and 4). Annual increases in coral cover on recovering reefs were low for 7–10 years following bleaching, but then increased substantially, probably reflecting increasing local recruitment levels necessary for rapid recovery in isolated coral communities[4]. In contrast, 9 of the 21 reefs followed a post-bleaching regime shift trajectory, with average macroalgal cover steadily increasing to 42% by 2011, coral cover remaining low (<3%), and benthic composition diverging substantially from the pre-bleaching state (Fig. 1c, Extended Data Table 1, Extended Data Figs 3 and 4). Percent cover of coral and macroalgae did not differ between these two groups of reefs in 1994 (Extended Data Table 1), providing the first clear evidence that regime shifts to macroalgae-dominated states occur in response to major coral bleaching events on Indo-Pacific reefs.

Divergent ecosystem trajectories following bleaching are likely to have major implications for reef associated organisms. The functional structure of communities, which captures species' roles based on their biological traits, is predicted to show deterministic links to disturbance[14], but predictions are rarely tested with data. Here we show changes to functional structure of reef fish assemblages are strongly tied to the post-bleaching benthic response (Fig. 2, Methods). Seven years after bleaching, assemblages on all reefs had fewer small bodied species and a less complex functional structure, typified by increasing dominance of invertebrate feeding fishes. On recovering reefs, a smaller initial change in functional structure was followed by a return towards the pre-bleaching state (Fig. 2b), whereas the much greater change on reefs that underwent regime shifts progressed in post-bleaching years, suggesting important functions are being eroded (Fig. 2c).

We assessed the association between 11 reef-level factors and ecosystem trajectories post-disturbance, a priori selected for their generic importance in structuring coral reef ecosystems globally (Extended Data Table 2). Five of the factors correctly (97% of the time) characterized post-bleaching reef trajectories as 'recovery' or 'regime shift': density of juvenile corals, initial structural complexity of the reef, water depth, biomass of herbivorous fishes (also reflecting herbivore diversity, which was collinear), and nutrient conditions of the reef (Fig. 3). Estimates of critical values for each factor, where recovery was more likely to occur than a regime shift, showed that juvenile coral densities >6.2 per m^2 reduce the probability of a regime shift (Fig. 3a), consistent with the expected role of coral recruitment and survival in reef recovery[4]. Coral larval supply does not differ among recovering and regime shifting reefs in Seychelles, but post-settlement survival is lower on regime shifted reefs[15], likely

due to unsuitable settlement substrate, or enhanced post-settlement mortality due to macroalgal overgrowth or alleopathic mechanisms[2,16]. Structural complexity, which captures the structure provided by corals and the underlying reef matrix, decreased the risk of a regime shift trajectory when values before disturbance were >3.1 (widespread moderately complex relief) (Fig. 3b). Structural complexity influences a range of ecological processes, being a substantial contributor to diversity and productivity of many reef associated organisms[17,18]. Sites deeper than 6.6 m depth were less likely to undergo a regime shift (Fig. 3c), possibly reflecting the relationship between light penetration and algal growth[19], or greater vulnerability of shallower reefs to disturbances such as recurrent coral bleaching or storm damage[20]. Experimental and modelling studies will be necessary to clarify the principal mechanisms by which structural complexity and depth influence ecosystem trajectories.

Reef fish herbivory is a key process mediating competition between corals and algae[21], and herbivore biomass, implicitly linked to body size, is a good proxy for overall rates of herbivory[22]. Interestingly, a relatively low biomass of herbivores (177 kg ha^{-1})—below average values for the Indian Ocean[23]—reduced the risk of a regime shift occurring (Fig. 3d). Algal proliferation and dominance over corals is also influenced by nutrient input to reef systems[24]. Here, lower C:N ratios in macroalgal fronds, indicative of higher nutrient loads[25], were linked to a greater likelihood of regime shifts, with the likelihood of regime shifts reducing below 50% when ratios passed 38 (Fig. 3e). Previous debate has focused on whether levels of herbivory or nutrients mediate coral reef regime shifts or recovery[26,27]. Our results suggest that although both variables relate to ecosystem trajectory, they are weaker and less certain predictors than structural complexity, depth, and the density of juvenile corals.

Reefs within no-take marine reserves were no more likely to recover than reefs in fished areas. Although marine reserves may have a positive long-term influence on coral cover in the absence of disturbance[28], our results suggest they may have little influence on post-disturbance benthic trajectories. In Seychelles, marine reserves do enhance herbivore biomass (2005 values: 279 kg ha^{-1} ± 21.5 s.e.) compared to fished areas (mean 163 kg ha^{-1} ± 58.6 s.e.), but biomass in fished areas was still close to the threshold we identified for recovery. Marine reserves may have a greater role in aiding coral recovery in nations where herbivorous fishes are more heavily exploited or where fishing gears that reduce structural complexity are used.

Collecting data on nutrients and juvenile coral densities can be challenging for the often resource-limited agencies charged with monitoring and managing coral reef ecosystems, especially over large areas. We therefore assessed the predictive power of structural complexity and water depth alone to predict reef trajectories. Both variables can be rapidly recorded over large areas and are relatively stable through time, allowing extensive pre-disturbance data to be compiled. Using only these two
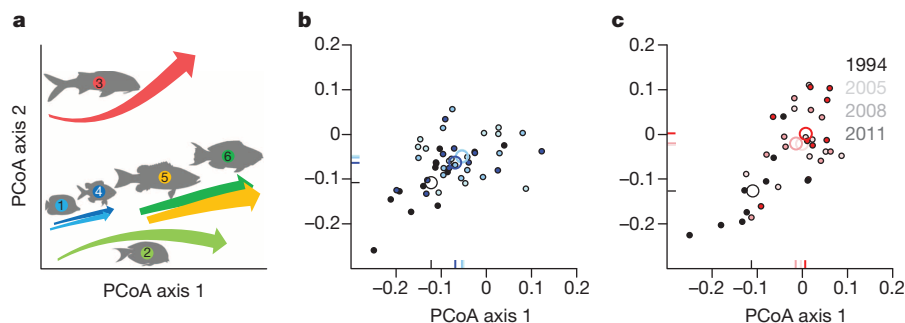

Figure 2 | Trajectories in the functional structure of fish assemblages.
a, Functional trait space underlying the analyses, with arrows depicting increasing body size amongst each fish functional group, depicted by fish outlines: corallivores (1), grazing herbivores (2), invertebrate feeders (3), planktivores (4), piscivores (5), scraping and excavating herbivores (6).
b, c, Position of recovered (**b**) and regime shifted (**c**) reef sites in the functional space. Black dots represent the mean trait values in 1994, pale to darker colours represent 2005–2011 (n = 84). Large rings indicate centroid for sites within each year (2005 and 2008 overlap in **b**). Dashes on the axes indicate centroid positions for each year. Year and ecosystem trajectory were significant factors (Methods, ANOVA model: axis 1 year $P < 0.001$, trajectory $P < 0.01$; axis 2 year $P < 0.001$, trajectory $P < 0.05$). Fish graphics by T. Saxby, D. Kleine and J. Woerner (Integration and Application Network, University of Maryland Center for Environmental Science, http://ian.umces.edu/imagelibrary/).
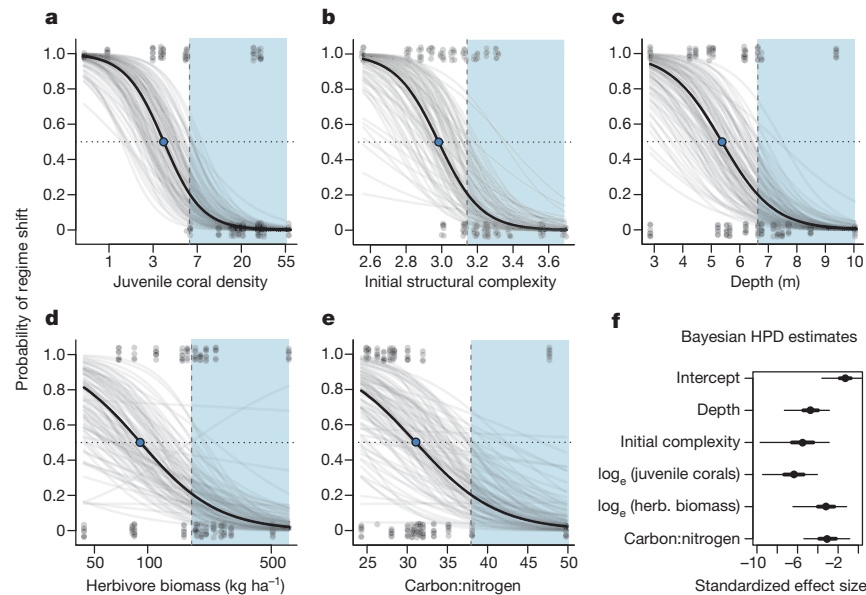
Figure 3 | Bayesian hierarchical logistic regression of predictor variables for the probability of a regime shift. a–e, Marginal plots for predictor variables included in the full model: solid black line represents the mean model fit; grey lines are random resamples of the parameter estimates, representing variability of the expected model fit. Grey dots represent replicates from regime shifted (1) or recovering (0) reefs ($n = 184$). The blue dot represents the point at which regime shifts and recovery are equally likely. Blue shading is beyond upper 95% uncertainty interval for P (shift) = 0.5, where regime shifts are decreasingly likely. **f.** Effect size medians (black dot), with 50% (thick line) and 95% (thin line) highest posterior density (HPD) uncertainty intervals.

variables, we correctly predicted reef trajectory 98% of the time. This suggests that, when combined, structural complexity and depth can effectively identify reefs with a high likelihood of recovery or regime shift, thereby informing reef risk assessment and guiding marine spatial planning initiatives (Fig. 4).

We have demonstrated persistent and divergent responses of coral reefs to climate-induced bleaching with potential consequences for reef fish functioning. With predictions that mass coral bleaching events will increase in frequency[1], our findings foreshadow the likely divergent trajectories expected on other Indo-Pacific reefs. We show that several factors can affect reef ecosystem trajectories following bleaching but, where

necessary, just depth and structural complexity may be useful predictors of ecosystem fate. The predictor factors we identify are important for coral reefs globally (Methods) and the range of values reported for Seychelles is consistent with other locations in the Indo-Pacific (Extended Data Table 3). Further, depth and initial structural complexity evaluated across 6 other countries from East Africa to the South Pacific were consistent predictors of coral or macroalgal dominated reefs post-disturbance, with effect sizes overlapping those from Seychelles (Extended Data Fig. 5). However, there may be regional variations in the relative contribution of factors and threshold values we identified that require more investigation. Uncovering the predictors that dictate reef trajectories following major bleaching events can inform ecosystem management and strategies for human adaptation. Mapping probable ecosystem trajectories can enable limited management resources to target actions, such as phasing out fishing gears that cause habitat damage[29], on reefs where increased structural complexity could help promote recovery[29]. Spatial understanding of ecosystem vulnerability to climatic impacts also holds great potential to be linked with social vulnerability assessments to develop the human adaptation strategies needed to cope with anticipated regime shifts and associated changes in ecosystem services[30].
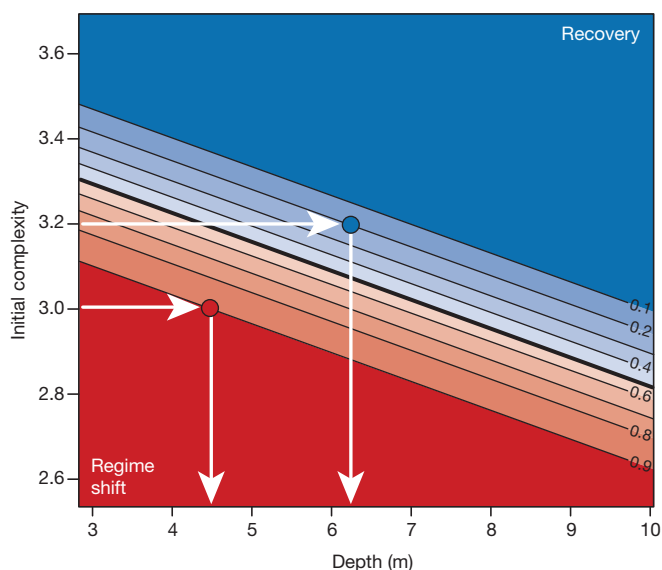
Figure 4 | Contour biplot of the probability of regime shift (red shading) or recovery (blue shading) based on initial structural complexity and water depth. For example, for a complexity value of 3, there is a 0.9 probability of a regime shift occurring for sites <4.5 m depth (red dot), and only sites deeper than ~8 m are more likely to recover. For a complexity value of 3.2, sites deeper than 6.3 m are highly likely to recover (blue dot).

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METHODS

Field Surveys and indices. Twenty one reefs throughout the inner Seychelles Islands were surveyed using identical methods in 1994, before the mass coral bleaching of 1998, and in 2005, 2008 and 2011, following the bleaching event. The surveys incorporated three different reef habitat types; carbonate fringing reefs; granitic rocky reefs with coral growth; and patch reef habitats on sand, rubble, or rock base. Eight to sixteen replicate 7 m radius point counts were surveyed along the reef slope on each reef, covering up to 0.5 km of reef front and 2,500 m² of reef habitat. The underlying substrate type and water depth were recorded at each site. Within each point count area, the percent cover of different growth forms of live hard coral, soft coral, macroalgae, sand, rubble, and rock was quantified, and the structural complexity of the reef was visually estimated on a 6 point scale[13]. This structural complexity measure captures landscape complexity, including the complexity provided by live corals, that of the underlying reef matrix and other geological features, and has been shown to correlate well to other measures of complexity, such as measures of reef height and the linear versus contour chain method[31]. The complexity of each individual count area was assigned to one of the following categories: 0 = no vertical relief, flat or rubbly areas; 1 = low (<30 cm high) and sparse relief; 2 = low but widespread relief; 3 = widespread moderately complex (30–60 cm high) relief; 4 = widespread very complex (60–100 cm high) relief with numerous fissures and caves; 5 = exceptionally complex (>1 m high) relief with numerous caves and overhangs. Estimates can be standardised among observers with minimal training, thereby providing reliable and comparable data of ecological relevance[31]. The density and individual sizes of 134 species of diurnally active, non-cryptic, reef associated fish were recorded within each point count area. Length estimation was calibrated at the beginning of each day by estimating the length of known lengths of PVC pipe. Accuracy was within 4% of actual lengths[32]. We converted data on fish counts to biomass with published length–weight relationships[33,34]. Fish were assigned to feeding groups based on their dominant diets and feeding behaviour[35]. The density of juvenile corals (<10 cm diameter) was quantified in 2011, within 8 replicate 33 cm by 33 cm randomly placed quadrats in each point count area. Juvenile coral data were also collected in 2008, and correlated strongly across sites with 2011 data ($r = 0.85$), suggesting that patterns in juvenile coral densities are fairly consistent through the post-disturbance years surveyed. Sea urchin density (family: Diadematidae) was counted in 2008 in each point count area. Meta-data from these surveys will be deposited in the James Cook University research data repository, the Tropical Data Hub (https://eresearch.jcu.edu.au/tdh).

To assess local nutrient levels ten fronds from each of ten different *Sargassum* thalli were taken from each reef site in 2014. These samples were dried for 48 h at 60 °C, powdered and analysed for nitrogen and carbon abundance. Carbon and nitrogen weight percent (%C and %N, respectively), and C:N ratios were determined using a Costech Elemental Analyzer fitted with a zero-blank auto-sampler at James Cook University's Advanced Analytical Centre, Cairns. The ratio of carbon to nitrogen in macroalgae is a stable, longer-term indicator of ambient nutrient regimes at a given location and should reflect stable spatial patterns among sites[25,36]. Specifically, nutrient inputs incorporated into algal tissue are averaged over the active growing period (3–6 months before our collection in this region[37]), reflecting nitrogen availability during this time[38]. This time period spans the main rainy season in Seychelles (December to February), so the nitrogen in these algal tissues should reflect land-based nutrient inputs. Although temporal variability in nutrient input is likely, due to differences in rainfall among years, the spatial patterns associated with adjacent land-based input among sites (that is, the relative differences in nutrient regimes we are interested in here) are thought to be stable through time[38,39].

Wave exposure was calculated based on the uninterrupted (by land or other reefs) distance winds can blow over the ocean to generate waves (fetch), coupled with data on wind speed and direction[40,41]. Larger waves develop with greater fetch and stronger winds. We added reef crest polygons to a base map of land mass[42], and rasterised the map at a spatial resolution of 55 m. Fetch values for each of our 21 reefs was calculated in 32 compass directions (each with an angular width of 11.25) using the Waves Toolbox for ArcGIS 10.2 (ref. 43). We restricted fetch calculations to a maximum distance of 500km around the Seychelles islands, reflecting wind generated wave energy for this isolated archipelago. We used hourly readings of both wind speed and direction from the Seychelles National Meteorological Service for every day of the post-bleaching period (1998 to 2011). Wave energy (in Joules) was calculated as a function of fetch, wind speed and direction[40,41]. We calculated average wave exposure for each reef based on hourly wave exposure estimates for the entire post-bleaching period, capturing information on strong and sporadic winds.

Benthic trajectory. Changes in benthic composition among sites and through time were examined using correlation-based principle components analysis, based on Euclidian distance. Data were log($x + 1$) transformed to account for some right skewness detected in draftsman's plots and normalized to ensure all metrics in the analysis were on a common scale. Eigenvectors were overlaid to identify direction and

contribution of the different variables to the patterns. We defined a regime shifting reef as one where post-disturbance macroalgal cover becomes greater than coral cover and trajectories through time indicate that cover of macroalgae remains high or is increasing. Recovering reefs, conversely, are defined as those reefs where post-disturbance coral cover becomes greater than macroalgal cover and trajectories through time indicate that cover of hard coral remains high or is increasing. To determine whether sites were regime shifting or recovering we used four metrics, the first based on a static cover estimate, while the other three reflect cover trajectories. These four metrics provide a comprehensive assessment of site status and trajectory. Sites must conform to metric 1 and at least one of the trajectory metrics (2–4) to be classified as either recovering or regime shifting.

(Metric 1) Percent cover of coral and macroalgae at last data point (2011). If coral cover is higher than macroalgal cover, and greater than the first post-disturbance survey (2005), the site is classified as recovering. If macroalgal cover is higher than coral cover and greater than pre-disturbance macroalgal cover (1994), the site is classified as regime shifting (Extended Data Table 1).

(Metric 2) The Euclidian distance between the pre-disturbance (1994) benthic composition, and that of 2005, 2008 and 2011 was calculated at a site level, to quantify if this distance was increasing or decreasing through time. A substantial change from 1994 and increasing distance through post-disturbance years indicates a regime shifting site, whereas declining distance through post-disturbance years is indicative of recovery (Fig. 1b, c, Extended Data Fig. 3).

(Metric 3) The rate of change in coral or macroalgal cover post-disturbance (2005–2011) indicates the trajectory of the site in terms of increasing coral versus macroalgae. If rate of coral cover increase remains stable or increases faster than rate of macroalgal cover the site is classified as recovering, and vice versa for regime shifting (Extended Data Table 1).

(Metric 4) Change in cover (coral and macroalgae) between 1994 and 2005, and 1994 and 2011 was calculated. If the net decline in coral cover becomes smaller between these two time periods, and change in macroalgae is negligible and static, the site is classified as recovering. If the net decline in coral cover remains large and static, and increases in macroalgal cover are becoming greater, the site is classified as regime shifting (Extended Data Fig. 4).

To visualize the regime shift and recovery dynamics, we quantified the site level relationships between distance from the pre-disturbance benthic composition and proportions of coral and macroalgae using a multinomial model of benthic composition (j), whereby percentages of coral, macroalgae, and other substrates ($100 \times \pi_{ij}$) at a given site (i) were predicted based on Euclidian distances (ED) for a given year:

$$\pi_{ij} = \frac{e^{\beta_{0j} + \beta_{1j}ED}}{\sum_{k=1}^{J}(e^{\beta_{0k} + \beta_{1k}ED})} \tag{1}$$

Parameters include an intercept (β_0) and slope (β_1) for ED in each of the habitat categories (j). This is a standard multinomial logit model, in this case run using the *nnet* package in R (http://www.R-project.org). To illustrate the progression of reef states, we ran the same model (1) for each post-disturbance survey (2005, 2008, and 2001) and represented uncertainty in model fit by sampling values from the maximum likelihood and estimated standard deviation of each parameter in (1) and plotting the resulting model fits (Fig. 1c and Extended Data Fig. 3). To better convey the progression of recovering and regime shifting reefs through time we rotated the ED predictor onto the y axis.

Fish functional structure. The functional structure of fish assemblages was calculated based on two dominant traits that capture a large proportion of the implicit functional roles played by reef fishes: dietary group and body size. We classified the fish into well-established feeding groups (corallivores, invertivores, planktivores, grazing herbivores, scraping and excavating herbivores, and piscivores) based on the literature[35] and Fishbase[34]. These groupings cover some of the main feeding functions performed by fishes on coral reefs, including mediation of coral:algae interactions, removal of sediments, and trophic control through predation. Body size is a trait that captures information related to the feeding ecology, energetic demands, and movement patterns in reef fish. For example, there are well established nonlinear relationships between body size and area of reef grazed by parrotfishes[22], while predators feed on prey in accordance to their gape size[7]. Furthermore, home range size and functional range size in reef fish is tightly correlated to body size, with larger fish feeding over a greater area[44,45]. Body size was coded into four categories: <20 cm, 20–40 cm, 41–60 cm and >60 cm. We focused on these two biological traits to specifically target functional traits[46].

Based on these two functional traits, we performed a principal coordinate analysis (PCoA) on a Gower distance matrix between species pairs to provide two independent synthetic axes that summarize species distribution within a trait functional space[47,48]. These two independent functional axes from PCoA, in combination with the species abundance matrix for all reefs in each year of sampling, were used to measure functional structure through biomass-weighted mean values for each

community. We used these biomass-weighted mean values for each PCoA axis to assess how the functional structure of a given assemblage changed through time for both recovering and regime shifting reefs. Year and trajectory (regime shift versus recovery) had a significant influence on the functional structure of fish assemblages on both PCoA axes (ANOVA model: axis 1 year $P < 0.001$, trajectory $P < 0.01$; axis 2 year $P < 0.001$, trajectory $P < 0.05$), whereas management (marine reserve versus fished) had no significant influence (ANOVA model: management axis 1 $P = 0.533$, axis 2 $P = 0.106$).

Predicting recovery versus regime shift dynamics. We assessed the ability of eleven different site level factors (habitat type, initial branching coral cover, juvenile coral density, depth, herbivore biomass, herbivore diversity, marine reserve status, nutrient regime, initial structural complexity, sea urchin density, wave exposure) to predict whether a site went on a recovery or regime shift trajectory. Each factor was a priori chosen based on a pre-existing rationale from the literature, to specifically target factors known to represent key processes or to structure coral reef ecosystems globally (Extended Data Table 2). Indeed, the generic importance of the selected variables on coral reefs is highlighted by specific review papers, for example: branching corals[49]; juvenile coral survivorship[2]; depth[20]; marine reserve status[50]; herbivorous fish biomass and diversity[21]; nutrient regime[51]; structural complexity[17]; and sea urchins[2]. Furthermore, the range of values found on Seychelles are consistent with values from other reef locations in the Indo-Pacific (Extended Data Table 3), indicating that the relationships we find should be generic, although we might expect location-specific variation in thresholds. We could not include some factors, such as turbidity and water currents (typically weak in Seychelles), however we were able to accurately predict ecosystem trajectory with the covariates included in the model.

Although some of the factors are not influenced over the time frames investigated here (for example, depth), or were constructed across time (for example, wave exposure), we had to make decisions on which time period to use for other factors. Branching coral cover, important for a range of reef fishes and other organisms[49], is particularly vulnerable to coral bleaching[52], so reefs with a high branching coral cover pre-disturbance may be expected to undergo extensive degradation, and thus we used data from 1994. We used pre-disturbance data for structural complexity because it can be maintained for many years post disturbance, ensuring the continuation of reef processes[13]. For both herbivorous fish biomass and diversity, we used data from 2005 to first account for any changes in these variables associated with the disturbance event itself[53], and second to reflect the amount of post-disturbance herbivory available to influence subsequent benthic responses. We were interested in post-settlement survival based on the juvenile coral density variable, so used data from 2011 to allow more (often slow growing) corals to make it through early life history stages. Sea urchin density (family: Diadematidae), would ideally be taken from 2005 to reflect herbivory available for post-disturbance benthic responses, however the first year of available data was 2008, which correlated well (coefficient 0.57) to subsequent years, suggesting spatial consistency through time. As noted above, spatial differences in our nutrient regime data should reflect long-term patterns. Collinearity among these predictor covariates was assessed (Extended Data Fig. 6), and herbivore diversity was excluded from the analysis due to collinearity with herbivore biomass.

The spatial distribution of sites following a regime shift or recovery trajectory was to some extent geographically clustered, but some sites in close proximity followed different trajectories (Extended Data Fig. 7). We used a Bayesian hierarchical logistic regression model to assess which site-scale variables were best at predicting the trajectory of the sites post bleaching (0 = recovered, 1 = regime shifted). Discarding variables with posterior densities centred on zero (suggesting no effect), our full model for regime shifts among Seychelles sites was:

$$y_{ij} \sim Bern(p_{ij}) \tag{2}$$
$$logit(p_{ij}) \sim N(\mu_j, \sigma) \tag{3}$$
$$\mu_j = \beta_0 + \beta_1 LHB_j + \beta_2 JCD_j + \beta_3 DEP_j + \beta_4 IST_j + \beta_5 CNR_j \tag{4}$$
$$\beta_{0,\dots,5} \sim N(0.0, 1000) \tag{5}$$
$$\sigma \sim U(0, 100) \tag{6}$$

which included log(herbivore biomass + 1) (LHB; $kg\,ha^{-1}$); juvenile coral density (JCD; m^2); depth (DEP; m); initial structural complexity (IST; 0–5 scale); and the carbon nitrogen ratio of sampled algae (CNR). Covariates were then standardized by subtracting their mean and dividing by 2 of their standard deviations to gauge their relative importance as the relative magnitude of their effect sizes. Models were run using the PyMC package[54] for the Python programming language (http://www.python.org).

For each of these variables, we calculated marginal 95% uncertainty intervals (UI) around the point at which the probability of a regime shift was half (P(shift) = 0.5). The lower 95% UI was taken as the point at which a regime shift is more likely than not, with all other variables held at their average, while the upper 95% UI was taken

as the point at which recovery is more likely to occur. The values within these uncertainty bounds reflect the unstable area where recovery or regime shift outcomes are equally likely.

In order to assess the predictive ability of the full model, we ran a leave-one-out cross validation (Loo-CV) analysis, a permutation procedure whereby the ability of the model to successfully predict the ecosystem trajectory (recovery or regime shift) of any given site is repeatedly tested with different sites. To do this we randomly selected one site and predicted its recovery or regime shift status using a model based on the other 20 sites, repeating the procedure 999 times.

We tested the predictive power of the model if reduced to include only two metrics (initial complexity of the reef and water depth), both of which can be easily quantified in surveys and collected on reefs before major disturbance events, making them very strong candidates for management planning and informing development of adaptation strategies. This gave a reduced parameter model:

$$y_{ij} \sim Bern(p_{ij}) \tag{7}$$
$$logit(p_{ij}) \sim N(\mu_j, \sigma) \tag{8}$$
$$\mu_j = \beta_0 + \beta_3 DEP_j + \beta_4 IST_j \tag{9}$$

We re-ran the Loo-CV analysis with this subset of predictor variables to assess the predictive power that was lost by removing other variables from the analysis. Despite the substantial increase in deviance information criterion (DIC) scores between models (Mfull DIC = 129; Msubset DIC = 145), the subset model performed equally well in correctly predicting the trajectory of our observed reefs. We sampled from the posteriors of the two variables from the subset model across their observed range to model probability surfaces of regime shift risk when these two metrics are both quantified, presented as a contour plot in Fig. 4.

To assess whether these two simple predictor variables (depth and initial structural complexity) are likely to be useful predictors of post-disturbance reef condition elsewhere in the Indo-Pacific, we compiled data from 6 countries (Australia (Great Barrier Reef), British Indian Ocean Territory (Chagos), Fiji, Kenya, Maldives, Tanzania)[55–58] where before disturbance site depth and structural complexity, and post-disturbance (average 8.4 years ± 0.4 post-disturbance) coral and macroalgal cover were recorded. The disturbances were mostly climate induced bleaching, but in combination with crown-of-thorns starfish (COTS) in Fiji and COTS and storms in Australia. For depth we used data from all 51 reef sites. However, because structural complexity can vary based on reef zone (for example, the reef slope versus the reef flat), or geomorphology (for example, atolls versus coastal fringing reefs), we used a paired design for assessing the role of structural complexity where a site that had become dominated by macroalgae was paired with a nearby similar site (for example, same zone, geomorphology, and depth) that had recovered to high coral cover. This resulted in 7 pairs ($n = 14$), from 4 of the countries. We ran the Bayesian hierarchical logistic regression model used for the Seychelles data, with reef sites assigned as having either higher macroalgal cover (1) or coral cover (0) post disturbance. The Bayesian effect size posterior density distributions for these wider Indo-Pacific data were compared to those for the Seychelles reefs (Extended Data Fig. 5). Considerable overlap in both the depth (Seychelles: -4.77 [-6.92, -2.62]; Indo-Pacific: -1.67 [-3.74, 0.15]; median and 95% highest posterior density uncertainty intervals) and complexity (Seychelles: -5.66 [-9.13, -2.69]; Indo-Pacific: -3.29 [-6.94, -0.25]) posterior distributions from the six Indo-Pacific countries with those from Seychelles, and more than 95% of the density in the posterior distributions falling below zero in all cases, suggests that both variables are important, generic predictors of macroalgal dominance post-disturbance on Indo-Pacific reefs. Interestingly, although the structure of reefs may vary based on zone or geomorphology, in 6 of the 7 pairwise comparisons, the reef with the greatest structure recovered. On average, reefs that recovered had complexity scores 0.85 (0.09–1.62 UI) greater than reefs than became dominated by macroalgae.

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Extended Data Figure 1 | Changing condition of Seychelles coral reefs.
a, **b**, Coral reefs of the inner Seychelles were typified by high coral cover and low macroalgal cover in 1994. **c**, **d**, The 1998 coral bleaching event caused widespread coral loss, but some reefs maintained their structural complexity (**c**), while others collapsed (**d**) by 2005. **e**, **f**, In 2011, many reefs had recovered to high live coral cover (**e**), while others had undergone a regime shift to abundant macroalgal cover (**f**).
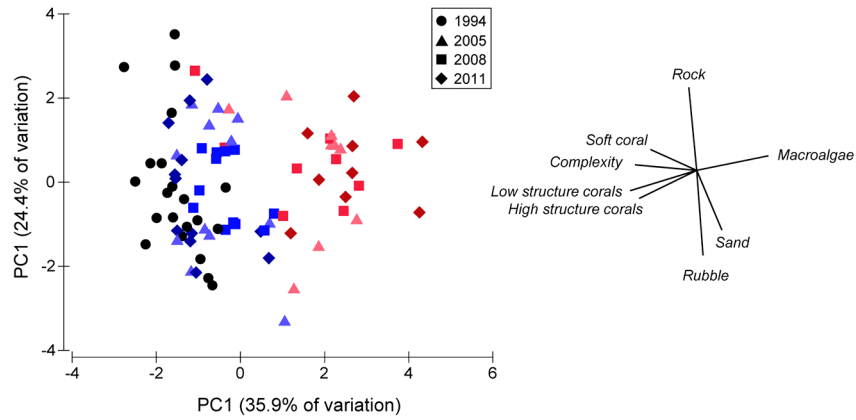
Extended Data Figure 2 | Principal components analysis of benthic composition on 21 reefs across the inner Seychelles 1994–2011. Reefs coloured blue are tracking back to pre-disturbance benthic composition in 2005–2011 following the 1998 bleaching event, whereas reefs coloured red are shifting to alternate benthic compositions, dominated by macroalgae ($n = 84$).
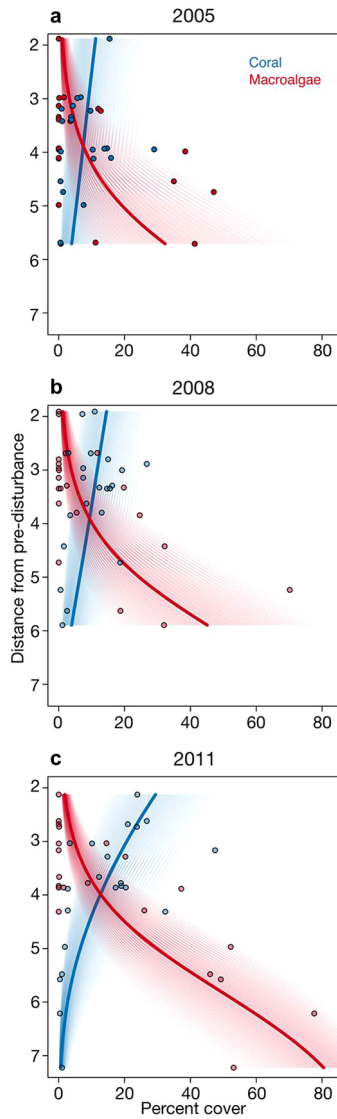
Extended Data Figure 3 | Distance from pre-disturbance benthic community composition. Euclidian distance in multivariate space, plotted against percent cover of dominant biotic benthic organisms (live coral in blue, macroalgae in red) ($n = 63$). **a,** 2005 data. **b,** 2008 data. **c,** 2011 data. Shading represents 95% confidence bounds for the mean trend lines of each habitat type.
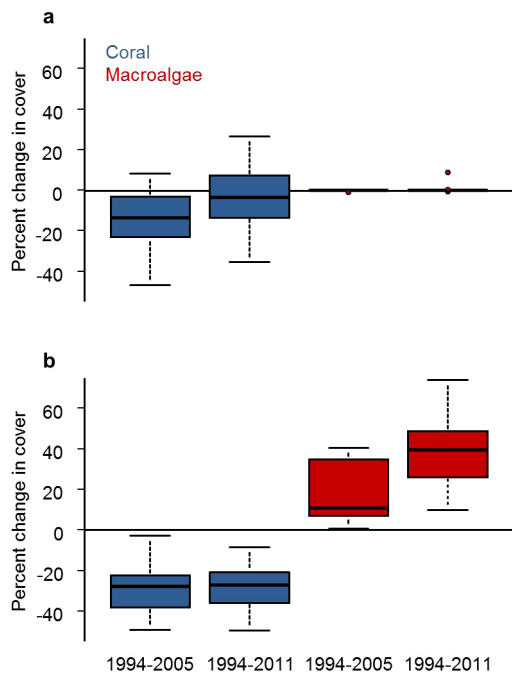
**Extended Data Figure 4 | Changing coral and macroalgal cover is relation to pre-disturbance values. a**, Data for recovering reefs, where the change in coral cover compared to 1994 was reducing through time, whereas change in macroalgae remained stable ($n = 42$). **b**, Data for regime shifting reefs where the decline in coral cover persisted through time, and changes in macroalgae increased through time ($n = 42$).
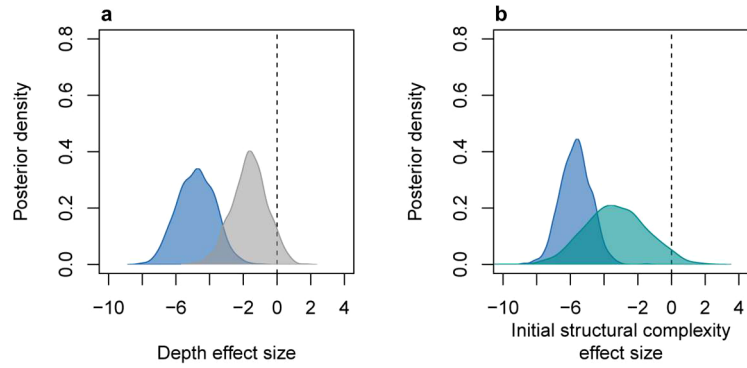
Extended Data Figure 5 | Comparison of effect size posterior density distributions for depth and initial structural complexity in predicting coral versus macroalgae outcomes post disturbance in Seychelles versus 6 other countries across the Indo-Pacific. a, Depth effect size plot, dark blue posterior distribution for Seychelles, grey for other countries ($n = 51$). **b**, Initial structural complexity effect size plot, dark blue distribution for Seychelles, green for other countries ($n = 14$). Depth and structural complexity variables were standardized in both analyses before estimation and all posterior distributions have more than 95% of their density below zero.
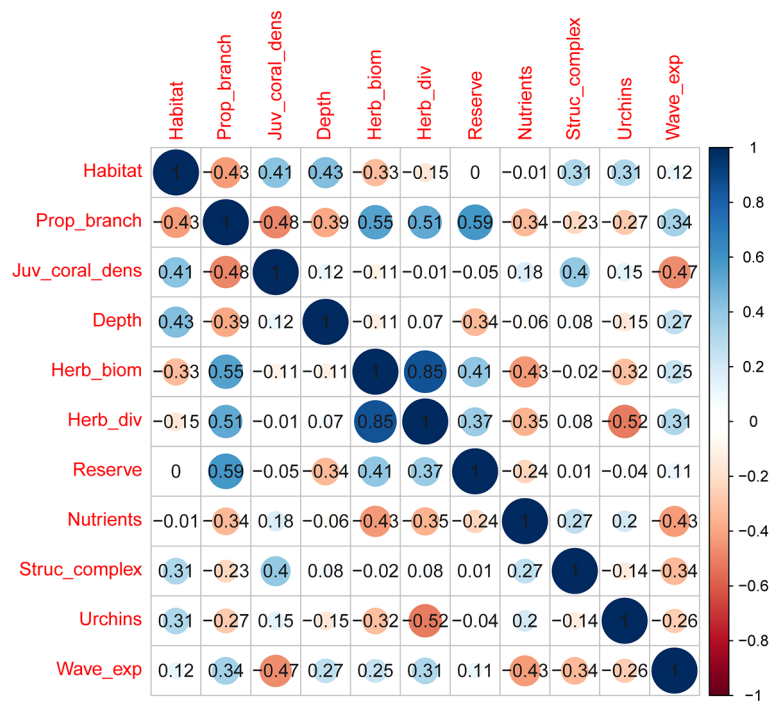
Extended Data Figure 6 | Collinearity matrix of the eleven predictor variables.
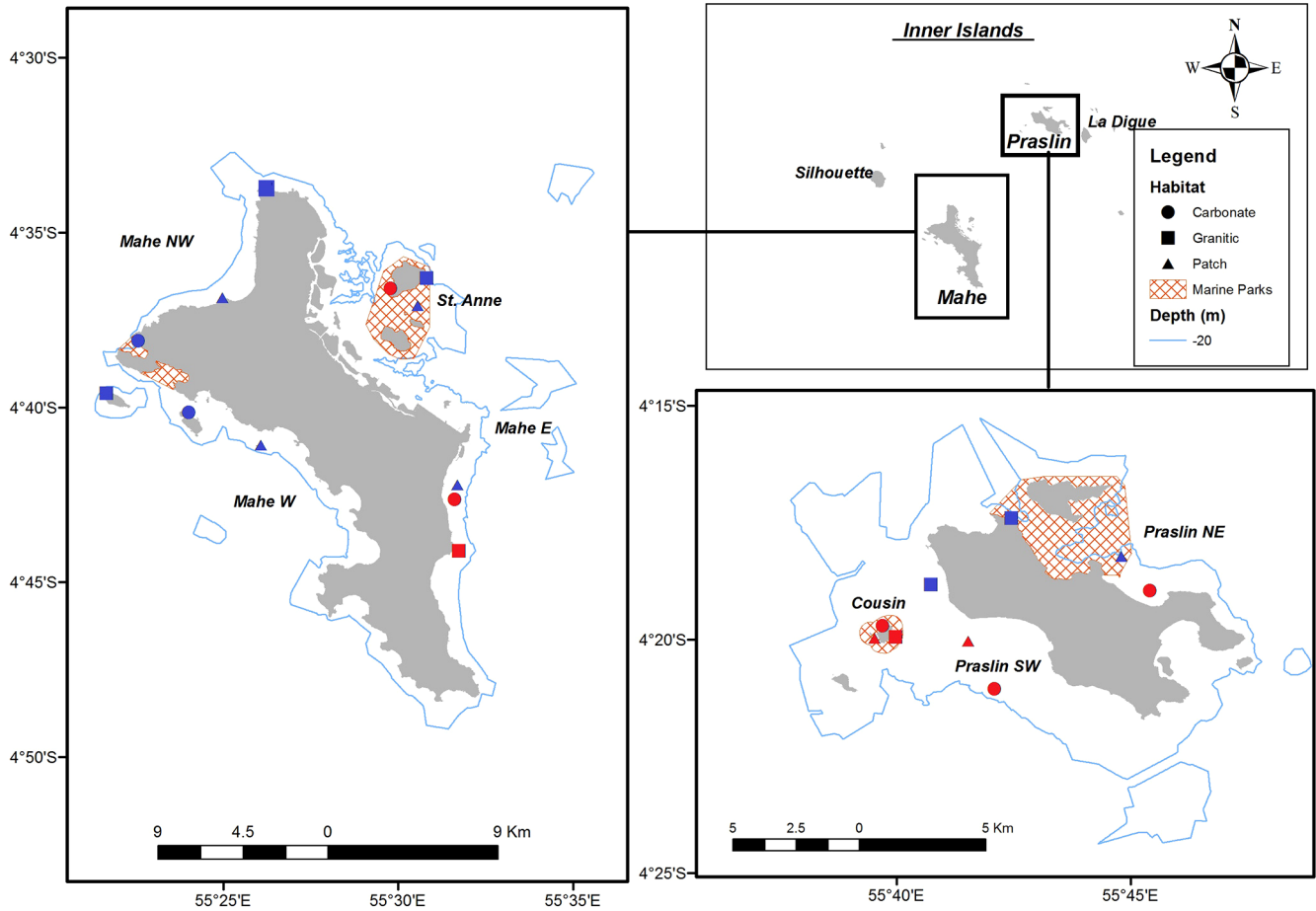
Extended Data Figure 7 | Map of study sites around the inner Seychelles. Sites in blue are recovering from the 1998 mass bleaching event, whereas sites in red have undergone a regime shift to macroalgal cover.

Extended Data Table 1 | Coral cover and macroalgal cover at recovering and regime shifting sites in 2011, with the change (based on the model slope) in coral cover and macroalgae estimates from sites between 2005–2011

	Coral cover (%) 1994	Coral cover (%) 2011	Coral slope 2005-2011	Macroalgae cover (%) 1994	Macroalgae cover (%) 2011	Macroalgae slope 2005-2011
Recovering sites						
Mahe E Patch	19.3	12.3	3.3	0.6	0.1	-0.8
Mahe NW Carbonate	38.9	26.8	8.2	0.0	0.0	0.0
Mahe NW Granitic	10.8	19.0	4.2	0.0	0.0	0.0
Mahe NW Patch	17.3	21.3	3.3	0.0	0.0	0.0
Mahe W Carbonate	34.9	23.9	4.2	0.0	0.0	0.0
Mahe W Granitic	19.3	32.4	8.3	0.0	0.0	0.0
Mahe W Patch	20.8	47.5	9.3	0.0	0.0	0.0
Praslin NE Granitic	17.1	23.8	10.0	0.0	0.1	0.1
Praslin NE Patch	25.4	10.1	2.9	0.0	0.0	0.0
Praslin SW Granitic	17.4	17.5	6.8	0.3	0.0	0.0
Ste. Anne Granitic	38.5	20.4	3.3	1.0	1.5	0.7
Ste. Anne Patch	54.2	18.9	5.7	0.0	8.8	4.4
Average	**26.1 ± 5.5 CI**	**22.8 ± 5.5 CI**	**5.8 ± 1.6 CI**	**0.2 ± 0.2 CI**	**0.9 ± 1.4 CI**	**0.4 ± 0.8 CI**
Regime shift sites						
Cousin Carbonate	49.7	0.4	-0.1	0.4	49.3	4.0
Cousin Granitic	23.3	2.8	0.8	0.6	37.3	16.8
Cousin Patch	38.6	2.8	1.1	0.0	26.0	-4.5
Mahe E Carbonate	28.6	1.9	0.3	12.4	52.3	2.6
Mahe E Granitic	9.3	1.0	-2.5	0.7	46.0	22.2
Praslin NE Carbonate	28.3	1.0	0.3	0.0	53.1	21.0
Praslin SW Carbonate	42.1	0.4	-0.1	3.4	77.6	19.6
Praslin SW Patch	17.3	3.4	1.3	4.7	14.5	1.3
Ste. Anne Carbonate	40.1	14.8	2.6	2.0	20.3	3.8
Average	**30.8 ± 8.5 CI**	**3.14 ± 2.9 CI**	**0.40 ± 0.9 CI**	**2.7 ± 2.6 CI**	**41.8 ± 12.8 CI**	**9.63 ± 6.6 CI**

Average values for coral cover and macroalgal cover in 1994 also given for recovering versus regime shifting reefs.

Extended Data Table 2 | Rationale for predictor variables included in models determining different post-disturbance reef trajectories on Seychelles reefs

Predictor	Rationale	References
Habitat type	Three habitat types were surveyed in Seychelles, including carbonate fringing reefs, granitic rocky reefs, and patch reef habitats. These habitats differ in their underlying matrix that may influence coral recruit success or likelihood of ecosystem collapse.	32,59,60
Pre-disturbance branching coral cover	Branching corals are particularly vulnerable to coral bleaching events, and once dead the structure they provide erodes fairly rapidly. Therefore, reefs with a high cover of branching coral before a disturbance may be particularly vulnerable to extensive coral loss and a reduction in other organisms.	52,61
Juvenile coral density	Successful settlement, survival and growth of new corals is thought to be key to coral recovery dynamics.	2,4
Depth	Many threats on coral reefs are worst in shallow water, making shallow areas most vulnerable to change. Light penetration in shallow water may also favour rapid growth of fleshy macroalgae.	19,20
Herbivorous fish biomass	Herbivorous fish are key to mediating competition for space among corals and algae. Biomass of these fish is a good proxy for function as the area of a reef grazed by these fish scales with both abundance and body size.	21,22,62
Herbivorous fish diversity	Many types of algae have defences against herbivores, meaning that only certain species of fish can feed on some species of algae. This differential ability of fish species to control algae, can mean that a diversity of herbivorous species is required to provide the feeding complementarity necessary to control macroalgae.	63-65
Marine reserve status	No-take marine reserves are expected to reduce fishing and hence enhance ecosystem processes, and may therefore promote faster rates of coral recovery.	28,66
Nutrient regime	Higher nutrient loads in the waters around reefs can enhance the growth of algae and result in algae outcompeting corals, particularly when space becomes available through coral mortality.	19,67
Pre-disturbance structural complexity	The structural complexity of a reef provides a great deal of the habitat variability for a diverse array of other organisms to inhabit. This in turn contributes to enhance a range of ecological processes, and provides niche space for coral settlement and survival. Structural complexity prior to a disturbance is expected to maintain ecosystem processes through the disturbance.	17,18,68
Sea urchin density	Sea urchins are important herbivores on coral reefs, helping to control algal growth and promote successful coral recruitment and recovery.	2,69
Wave exposure	Wave exposure influences coral distribution patterns, growth forms and colony sizes that will likely affect recovery trajectories. Similarly, algal growth can be enhanced with higher flow rates due to increased exposure to water borne nutrients, but algal dislodgement can occur where wave exposure is strong.	70-72

Including references 59–72.

Extended Data Table 3 | Mean values with 95% confidence intervals for predictor covariates in Seychelles compared to other coral reef locations where similar data for the covariates were available

	Seychelles	95% CI	N	Other locations	95% CI	N	Countries
Herbivore biomass	210.3	59.0	21	258.1	33.8	281	Kenya, Madagascar, Maldives, Mauritius, Mayotte, Reunion, Tanzania
Pre-disturbance coral cover	28.1	5.4	21	29.0	3.9	60	Kenya, Tanzania
Pre-disturbance structural complexity	3.2	0.1	21	3.1	0.2	30	British Indian Ocean Territory (Chagos), Great Barrier Reef (Australia)
Urchin abundance	2.2	0.8	21	4.1	2.0	33	Kenya, Madagascar, Mozambique, Tanzania

Data for regions other than Seychelles were provided directly by the authors of these studies[23,73,74].