Fine-scale interplay between decline and growth determines the spatial recovery of coral communities within a reef

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Open Research statement

Data are already published and publicly available, with those items properly cited in this submission. Data sets utilized for this research are as follows: `https://doi.pangaea.de/10.1594/PANGAEA.907025` (Roelfsema et al., 2019) and `https://doi.org/10.6084/m9.figshare.14034320.v1` (Roelfsema et al., 2021a).

Model codes are available at: `https://github.com/JulieVercelloni/spatio-temporal_modelling`.

Keywords

Branching coral, Coral cover, Disturbance, Plate coral, Resilience, Spatial scales, Spatio-temporal modelling

Abstract

As coral reefs endure increasing levels of disturbance, understanding recovery patterns of reef-building hard corals is paramount to assessing the sustainability of these ecosystems. At local scales, coral recovery slows down; however, it's unclear how this trend propagates across spatial scales due to the inherent complexity of coral dynamics. In this paper, we aimed to learn about fine scale heterogeneity of coral dynamics and explore implications for assessing coral recovery at larger spatial scales. We developed a spatio-temporal statistical model to estimate long-term trajectories of three types of corals and predict their recovery patterns at unobserved locations within a reef. Then, model predictions were used to derive metrics that capture the interplay between coral growth and decline from disturbance(s) across time, space and growth morphology. This model is developed in the context of a substantive case study at Heron Reef using a high spatio-temporal resolution dataset. Our results revealed that successful coral community recoveries took place in different habitats of Heron Reef and associated with various reasons. Branching corals recovered in the southern slope, due to fast growth in locations that were previously abundant. Plate corals flourished in the northern slope due to fast growth, despite a large decline and low baseline cover. They also recovered in the southern slope but in this case there was both a low decline and baseline cover. At Heron Reef, the recovery of coral communities followed specific conditions that were acting at a fine scale in a complex and heterogeneous way within habitat. This implies that capturing the

variability of fine-scale coral dynamics is an important first step to detect accurate signals of coral recovery at larger spatial scales. The approach proposes here can be further extend to the scale of a reef and beyond enabling assessment of recovery patterns representative at management scales.

Introduction

The data revolution provides new opportunities to estimate changes in biodiversity as climate change unfolds (Dornelas et al., 2023). However, it has been shown that patterns of change can exhibit contradictory trends depending on spatial scales (Pereira et al., 2012; De Palma et al., 2018; Dornelas et al., 2023). One example of complexity inherent in this problem is long-term trajectories of hard coral communities on the Great Barrier Reef that show opposite trends between sites separated by 100 meters only, resulting in high uncertainty in coral trends at larger spatial scales (Vercelloni et al., 2017; Mellin et al., 2019b). The fine-scale variability of coral dynamics complicates understanding of community changes and associated drivers of change at regional and global scales despite important progress in the estimation of status of coral reefs worldwide (Souter et al., 2021).

Branching and plate corals play a critical role as reef builders providing habitats for a myriad of organisms living upon them (Kerry and Bellwood, 2012; Darling et al., 2013). It is therefore imperative to understand the dynamics of these coral types. Of particular interest is coral recovery in response to cumulative impacts of chronic and acute stressors (Adjeroud et al., 2009; Fisher et al., 2015; Kayal et al., 2018; Ortiz et al., 2018; Darling et al., 2019) which may be accentuated by large-scale, climate-driven disturbances that spatially isolate disturbed from undisturbed reefs across hundreds of kilometres (Hughes et al., 2018; Dietzel et al., 2021) and inhibit connectivity and coral recruitment (Hughes et al., 2019). Patterns of coral reef recovery are driven by various variables acting at different spatial scales, such as aspects of recent and past disturbance(s) (Connell et al., 1997; Graham et al., 2011, 2015; Ortiz et al., 2018; Mellin et al., 2019a), community structure and demographic processes (Gilmour et al., 2013; Adjeroud et al., 2017; Kayal et al., 2018; Holbrook et al., 2018; Darling et al., 2019), and the environmental climatology of the habitats (Connell et al., 1997; Gouezo et al., 2019; Castro-Sanguino et al., 2021; Tebbett et al., 2022). Understanding the impact of these drivers may enable more accurate prediction of recovery dynamics of different communities and provide targeted information to assess recovery progress towards pre-disturbed states within monitoring locations (Johns et al., 2014; Kayal et al., 2018; Mellin et al., 2019a; Darling et al., 2019; Gouezo et al., 2019).

Spatial patterns are typically estimated at discrete hierarchical spatial scales, including sites, reefs, habitats and regions where comparisons are made between reef locations that have received different levels of stressors. This popular "space-for-time substitution approach" tends to overestimate reductions in population abundance, diversity and composition compared to more controlled sampling designs such as before-after-control-impact studies (De Palma et al., 2018; Dornelas et al., 2023). Overestimation may arise when monitoring observations are too narrow with respect to types and exposures of stressors and not sufficiently representative across the combination of reef habitats where different coral communities are found. This potential bias, in conjunction with the high uncertainty in coral trends at broad spatial scales, provides further motivation for exploring the influence of space in reef data.

Obtaining accurate and robust information on coral community recovery is one of the core challenges that need to be tackled to support management interventions in the light of complex spatio-temporal dynamics and new environmental regimes (Cumming et al., 2017; Anthony et al., 2020; Condie et al., 2021). An alternative approach to space for time substitution is to model the spatial and temporal dynamics directly. By representing the space using continuous spatial processes, we allow information sharing between nearby locations and introduce a dependence (defined as spatial auto-correlation) into the observed data. This spatial dependency can be used to capture the fine-scale variability of coral dynamics and estimate the spatial scale at which coral recovery patterns occur. It can also be used to estimate drivers acting at the fine scale, such as coral larval supply, coral recruitment and herbivory, in shaping those patterns (Hamylton, 2013; Edwards et al., 2017) as well as providing insight into reef accretion-erosion balance (Jackson-Bué et al., 2021).

In this paper, we introduce a spatio-temporal model to (1) estimate long-term trajectories of three types of hard corals at the scale of meters, (2) extract the spatial auto-correlation from the data, (3) use this information to predict coral cover at unobserved locations and (4) develop metrics from model predictions that capture the interplay between coral decline from disturbance(s) and growth across time, space and coral growth morphology. This model was developed in the context of a substantive case study. Since 2002, benthic communities have been monitored annually across different habitats at Heron Reef, situated in the Southern Great Barrier Reef (Roelfsema et al., 2021b). These surveys have captured 11 years of coral recovery (2008 - 2018) following the impacts of the white syndrome coral disease outbreak and storm damage. We aim to learn about fine-scale heterogeneity of coral dynamics during recovery, and the associated implications for assessing recovery patterns at the scale of a reef and beyond.

Methods

Heron Reef Survey

The ongoing Heron Reef Survey was originally designed to develop annual benthic habitat maps of the coral reef by integrating field image-based data and satellite imagery (Roelfsema and Phinn, 2010). The method uses geo-referenced photoquadrats collected at 2 - 3m intervals along random transects, where each photoquadrat represents a 1x1 m^2 footprint of the benthos (see Roelfsema et al. (2021a) for additional details on the methodology). Random transects are deployed within different habitats defined by geomorphic zones. These zones were defined by physical attributes including depth and wave exposure (Kennedy et al., 2020a; Roelfsema et al., 2021a). Heron Reef is divided into four habitats (Figure 1a): the northern and southern reef slope areas are characterized by high and low wave intensities, respectively, and depth of 4 - 7m; the inner and outer reef flat are shallower areas (0 - 2m) without influences of wave exposure. Importantly for the purposes of our study, these four habitats exist within close spatial proximity of each other.

The composition of benthic communities is estimated from photoquadrats using machine learning algorithms (González-Rivero et al., 2020; Roelfsema et al., 2021a). In this study, coral communities were aggregated into branching, plate and massive coral types to produce relative abundances of each coral type by photoquadrat. Sub-sites were defined as areas of 100 m^2 in size in each surveyed year and generated using hierarchical clustering based on Euclidean distance between geo-located photoquadrats. This method of data aggregation has been previously used to forecast the effects of cumulative disturbances in the northern GBR (Vercelloni et al., 2020), assess the efficiency of management zoning in Indonesia (Kennedy et al., 2020b) and the identification of hotspots of coral cover across Heron Reef (Roelfsema et al., 2021b).

Following this method, we generated 783 sub-sites across Heron Reef based on an average of 8.7 (± 4.6 standard deviation) photoquadrats per sub-site. The proportions of branching, plate and massive corals were then averaged within each sub-site across 16 years (2002 - 2018) and incorporated as a response variable into the statistical model.

Spatio-temporal model for coral cover

There is a growing body of literature demonstrating the importance of including the spatial structure of reef data in the assessment of the dynamics of coral cover (Levy et al., 2018), reef communities (Hamylton, 2013; Edwards et al., 2017; Aston et al., 2019; Ford et al., 2021) and habitat (Jackson-Bué et al., 2021). These papers employed various methods to characterize spatial auto-correlation and hence to gain knowledge about the spatial scales on which biotic and abiotic drivers are acting. In the following, we develop a spatio-temporal model to go beyond these approaches, with the goal of reusing the estimated spatial structure to interpolate coral cover at unobserved locations and thus increase the volume of information to interpret. This aim is the essence of modern spatial statistical modelling: to estimate spatial patterns while considering the effects of drivers in species responses, and interpolate over a continuous spatial field to predict responses at unobserved locations (Lindgren et al., 2011).

The aim of our Bayesian spatio-temporal model is to estimate long-term trajectories of three groups of corals from 2002 to 2018 (Eqs. 1). The coral cover $y_{it} \in (0,1)$ for observation i sampled at location s_i and time t was modelled independently for branching, plate and massive corals.Since the observed values of coral cover are proportions bounded between 0 and 1, we use a Beta likelihood to represent the observation process. This ensures that predictions generated by our model will be appropriately constrained, avoiding issues with negative values that otherwise might arise. The Beta likelihood is parameterized in terms of an overall precision parameter ϕ and linked to the linear model components via a logistic transformation, also known as an inverse-logit (Ferrari and Cribari-Neto, 2004).

$$
\begin{aligned}
y_{it} &\overset{\text{ind}}{\sim} \mathsf{Beta}\left(\phi, \text{logit}^{-1}(x_i^T \beta_j + r(s_i,t) + V_i)\right), \\
r(s_i,t) &= \omega \cdot r(s_i,t-1) + Z(s_i,t), \qquad (1)\\
Z(s,t) &\sim \mathscr{GP}(0,K), \quad t = 2002,\dots,2018
\end{aligned}
$$

where explanatory variables x_i have been transformed into dummy values encoding the four habitats, β_0 is an intercept term, $\beta_1,\dots,\beta_4$ represent fixed effects of each habitat, and V_i are independent random effects at the sub-site level. The spatio-temporal random effects $r(s_i,t)$ comprise a first-order autoregressive process in time, $\omega \cdot r(s_i,t-1)$, and a Gaussian process $Z(s,t)$ that is approximated using a Gaussian Markov random field (GMRF) and a covariance kernel, K. The GMRF approximation uses a stochastic partial differential equation approach (Lindgren and Rue, 2015). Under this approach, spatial covariance is assumed to be isotropic where only the distance between two observations is used to estimate their correlation (Gómez-Rubio, 2020). See Appendix S1 for detailed information about the spatio-temporal modelling.

Metrics of coral recovery

The years of recovery were set from 2008 to 2018 because no coral loss attributable to documented disturbances was reported during this period. Coral recovery followed the impacts of four years of white syndrome disease outbreak between 2004 - 2008 and storm damage in 2008 (Haapkylä et al., 2010; Roff et al., 2011). Despite the proximity of cyclone Hamish in 2009, there was no recorded impact on Heron Reef (Haapkylä et al., 2010).

Probability of recovery

In this paper, recovery is defined as the capability of branching and plate corals to recover from disturbance(s) to within 80 % of pre-disturbance cover values. The uncertainty associated with this outcome is encapsulated into the estimation of the probability of recovery, calculated from the respective posterior distributions obtained from the model. For every unobserved location $\hat{s}_i$, and coral morphology, the probability of recovery, $\hat{p}_{\text{rec}}$, is estimated from the difference between predicted coral cover at time t of recovery (2008 - 2018) and 80 % of their baseline cover (Eq. 2). The baseline, $\widehat{y}_{\text{baseline}}$, corresponds to the maximum coral cover that was predicted by the model during the pre-disturbance period of 2002 - 2007.

$$\hat{p}_{\text{rec},t} = \frac{1}{N}\sum_{k=1}^{N} 1\left\{\left(\widehat{y}_t^{(k)} - 0.8\widehat{y}_{\text{baseline}}^{(k)}\right) > 0\right\}, \quad t = 2008,\ldots,2018,$$

$$\widehat{y}_{\text{baseline}} = \max_{t\in\{2002,\ldots,2007\}} \widehat{y}_t, \tag{2}$$

with N corresponding to 2000 draws from posterior distributions of estimated coral cover $\widehat{y}_{\hat{s}_i t}$.

Recovery was asserted when $\hat{p}_{\text{rec}}$ was greater than 0.75 at any time during the years of recovery and locations $\hat{s}_i$. When this condition was satisfied, recovery was defined as successful. As such, successful recovery is interpreted as "75 % chance of recovering to at least 80 % of baseline coral cover."

Coral growth and decline

growth is defined as the difference in percent cover between two consecutive periods. Our intention is to investigate changes in proportion of coral cover from t to $t-2$ from 2010 to 2018 (Eq. 3). Coral decline is expressed as the amount of coral loss relative to the baseline cover. Coral cover estimated in 2008 is used in the estimation of coral decline as the major coral disease outbreak occurred between 2004 - 2008 (Haapkylä et al., 2010; Roff et al., 2011).

$$\begin{aligned}\mathsf{Growth}(t) &= \frac{1}{N}\sum_{k=1}^{N}\left(\widehat{y}_t^{(k)} - \widehat{y}_{t-2}^{(k)}\right), \quad t = 2010,\ldots,2018,\\ \mathsf{Decline} &= \frac{1}{N}\sum_{k=1}^{N}\left(\widehat{y}_t^{(k)} - \widehat{y}_{\text{baseline}}^{(k)}\right), \quad t = 2008,\end{aligned} \tag{3}$$

with N corresponding to 2000 draws from the predictive posterior distributions and $\widehat{y}_{\text{baseline}}$ as defined above in (Eq. 2). The posterior median coral growth and decline and associated 95 % credible intervals are estimated using the percentiles (50 %, 2.5 % and 97.5 % respectively) of their respective distributions.

Thresholds of recovery

We use estimates of coral growth and probability of recovery to determine minimum growth thresholds that ensured recovery. To do this, we developed logistic models for branching and plate corals where probabilistic outcomes of recovery were transformed into binary data with 1 when $\hat{p}_{\text{rec}}$ were greater than 75 % and 0 otherwise. The default threshold of 50% is used when interpreting the probabilities predicted by the logistic models. Models are fit on predictions from the reef slope south locations for branching corals in 2014 and reef slope north locations for plate corals in 2016. We assume that these years matched with the beginning of the exponential phase of coral growth as described in Ortiz et al. (2018).

Implementation

Spatio-temporal Bayesian model

Outputs from the spatio-temporal models are used to predict values of coral cover across the entire Heron Reef. To do this, the reef was divided into a grid of 2,384 locations (Figure 1b) and predictive values estimated for each of these new locations and surveyed years. The presence of residual spatial and temporal auto-correlation was tested using the DHARMa (Hartig, 2019) and glmmTMB (Brooks et al., 2017) R packages (Appendix S1). The spatio-temporal model was implemented using the r-INLA package (Rue et al., 2017) and run on a high-performance computer. The best model formulations were retained using visual and statistical diagnostics including model fit, residual patterns, basis dimensions, distributional assumption, and Akaike Information Criterion (AIC) values. Auto-correlation tests, computational details of fitting the models, as well as prior specifications, are provided in Appendix S1.

Metrics of recovery

Metrics are estimated at 2384 predictive locations s_i across Heron Reef but interpreted within a smaller area on the western side of the reef (Figure 1b). This area corresponds to the geographical extent of the data and included 481 locations. This step ensured the detection of signals from metrics of recovery due to a higher uncertainty associated with the spatial predictions at locations further away from the data (Appendix S2). Metrics were also estimated at the habitat scale by averaging values within the same habitat and associated uncertainty for a given year. The logistic models were developed using the R package ”brms” (Bürkner, 2017) and thresholds were estimated by averaging model outputs from 100 model iterations (Appendix S2).

Results and Discussion

Temporal changes of coral communities

Pre-disturbance (2002 - 2008)

In the period 2002-2008, before the major environmental disturbance(s), branching corals were abundant in the southern and northern slopes of Heron Reef (Figure 2a). The maximum coverage is estimated at 37.3 % (27.6 - 47.4 %, 95 % CI) in 2004 and 24.9 % (17.1 - 33.8 %) in 2006, respectively. A sizeable decline of branching corals is estimated in these habitats, with 93.4 % loss (86.8 - 97.3 %) in four years for the south slope and 83.5 % loss (71.8 - 91.9 %) in five years for the northern slope.

During the pre-disturbance period, plate corals dominated the northern slopes with maximum coverage of 26.4 % (19.4 - 34.0 %) in 2004 (Figure 2b). The relative decline from its cover baseline is estimated at 70.8 % (58.3 - 72.7 %). Studies by (Haapkylä et al., 2010) and (Roff et al., 2011) described the extirpation of corals, including plate corals during the major disease outbreak in 2004-2008 at different sites within these habitats. At the end of the outbreak, a shift in coral composition from plate to bushy corals was also recorded (Haapkylä et al., 2010; Roff et al., 2011).

Post-disturbance (2008 - 2018)

During the recovery period, branching corals mostly grew in the sheltered areas of the Reef Slope South that are protected from high wave exposure by adjacent reefs (Connell et al., 1997). In this habitat, coral cover is estimated to have increased from 2.5 % (0.9 - 4.9 %) in 2008 to 40.2 % (31.9 - 48.7 %) in 2014. In the northern slope, branching corals decreased until 2011 and then increased but in a lesser extent than in the south. This lack of growth for branching corals may be explained by the prominent increase of plate corals on the Reef Slope North which may benefited from the available space and favourable environmental conditions to grow (Figure 2b).

Plate corals grew in the southern and northern slopes of Heron Reef to reach maximum values that were higher than pre-disturbance values (Figure 2b). The prominent increase for plate corals occurred on the Reef Slope North, which is more exposed to frequent and higher intensity waves than the southern reef slope. In the northern slope, plate corals increased to 27.1% (20.9-33.7%) in 2018 and 18.1% (13.3-23.5%) in 2016 for the south habitat.

Through the years of recovery, coral community composition changed with a net dominance of plate corals in the northern section of the reef. The lack of recovery for branching corals cannot be explained by the nature of the disturbance as there is no clear evidence of what had impacted this reef section (Haapkylä et al., 2010; Roff et al., 2011). Differences in wave exposure between north and south and the high baseline prevalence of branching corals in the southern reef slope may have contributed to the rapid southern recovery due to their strong capability of recovery after fragmentation (Lirman, 2000). The study from Connell et al. (1997) indicated differences between mechanisms of declines and recoveries in northern and southern sections of Heron Island. Our results suggest that plate corals were able to recover from disease outbreaks, but this is less evident for branching corals on the northern slope. Coral colony size is an important factor associated with this type of disturbance (Roff et al., 2011), but the size was not recorded as part of the Heron Survey.

Spatial metrics of coral recovery

Interplay between recovery and coral growth at the habitat scale

Coral recovery is defined when a reef location reached 80 % of its baseline value. The rapid recovery of branching corals in the southern slope is well reflected by the dynamics of the probability of recovery, showing low chance of recovery during the first three years followed by high change of recovery (Figure 3a). In these locations, a ten-fold growth is estimated in four years, increasing from 0.05 % (-2.2 - 1.8 %) to 10.4 % (7.5 - 13.3 %, Figure 3b). Thereafter, the growth decreased to negative values reaching 4.5 % (6.8 - 2.4 %) in 2018. This decline in branching growth is likely related to a reduction in space availability during the years of recovery. The probability of recovery remained low for the northern slope habitat (Figure 3a), associated with a negative growth rate at the beginning and end of the surveyed years and a positive growth rate ranging between 1 - 2 % between these years (Figure 3b). For the remaining habitats, branching growth fluctuated between negative and positive values close to zero (Figure 3b).

On the south slope, the probability of plate recovery is estimated at 98.3 % (86.8 - 99.8 %) in 2008 and remained above this value until 2018 (Figure 3c), despite a low growth throughout these years estimated at 2-3 % (Figure 3d). On the north slope, the probability of recovery was almost zero for the first four years of the recovery phase and increased rapidly between 2012 and 2014 to reach the threshold of recovery in 2014 (Figure 3c) with an associated twelve-fold growth increase estimated between 2008 to 2014 (Figure 3d). This dynamic showcases the signature of plate corals. Indeed, these corals use the first years of recovery to build the base of their colony and then expand exponentially due to high growth rates and potential large sizes associated with their growth morphology (Ortiz et al., 2021).

Fine-scale interplay between coral growth, decline and cover baseline

At Heron Reef, branching corals recovered at 51.6 % of the fine-scale predictive locations across the north and south reef slopes in 6.90 years (± 1.25 SD). Our results show an unbalanced spatial recovery with 82.3 % of locations recovered in south slope and 14.2 % in the north (Figure 4a). In the locations that recovered, the average baseline cover was similar between south and north slopes, at around 33 % coral cover, but with a more uniform distribution for the southern locations where the cover baseline ranged from 20 % to 70% at 100m spatial scale (Figure 4b). These differences are also shown in the standard deviation of baseline cover distributions estimated at 3.2 and 16.8 % for north and south slopes, respectively. A higher heterogeneity in coral decline is captured in the southern slope habitat with an average decline of 25.5 % coral cover (± 0.11

SD) and 11.6 % decline (± 0.04 SD) in the north (Figure 4c). Interestingly, a similar range of coral growth is estimated between the two habitats during these years of recovery ranging from -16 % to 20 % (Figure 4d). However, the coral values for the southern locations were more highly concentrated around zero, indicating more homogeneous growth for this habitat (Figure 4d). The presence of more than one mode in the distributions of cover baseline, coral decline and growth estimated in the northern slope habitat may be a sign of very fine-scale drivers of coral dynamics splitting adjacent locations into groups. These locations are within a distance of 300 meters so it is possible that a physical barrier may have influenced the split; however, additional investigations are needed to interpret the origin of these distributions. In the southern slope, successful recovery were associated with a growth threshold of 4.30 % estimated from the logistic regression (Appendix S2). More than 75 % of locations situated in south slope reached this growth value only two years after the beginning of the recovery independently of their cover baseline and coral decline.

The recovery of plate corals was more evenly spread across the north and south slopes (Figure 5a), with 85.5 % of locations showing recovery in 6.87 years (± 2.43 SD). In locations that recovered, the average baseline was higher in south slope (estimated at 33.1 % ± 0.17 SD) compared to the north slope (18.9 % ± 0.08 SD). Similar to the branching corals, the range of cover baseline values was higher in the south compared to the north (Figure 5b). The decline was more pronounced in northern locations, with two modes appearing at 55 % and 10 % loss (Figure 5c). Plate loss in the southern slope was lower with an average of 27.7 % ± 0.12 SD. Growth values were higher in the northern slope with some growth values greater than 20 % (Figure 5d). In this habitat, the growth threshold that ensured recovery is estimated at 6.4 % (Appendix S2). Only 22 % of locations reached these growth values in 4–6 years. Overall, plate corals grew faster in the northern slope despite a low cover baseline and high decline. In a paper dedicated to tabular *Acropora*, Ortiz et al. (2021) describes the complex mechanism of coral settlement that is enhanced by the presence of dead colonies. Plate corals were mostly impacted by coral diseases that are known to preserve the dead skeletons of the corals on which potential new recruits can settle.

Learning from spatio-temporal coral dynamics

The presence of spatial and temporal auto-correlation in the long-term data of Heron Reef was demonstrated a long time ago by Connell et al. (1997). In this study, we refined this knowledge by quantifying spatial dependence during the recovery of different forms of corals after accounting for the influence of different habitats defined by geomorphic zones. Our findings show that the spatial auto-correlation is within the same range as that estimated by Connell et al.

(1997) - up to 800 m - but that this varies by coral morphology. Spatial ranges were estimated as 1.02 km (0.75 - 1.30 km, 95 % CI), 1.46 km (1.07 - 1.90 km) and 12.76 km (7.24 - 18.97 km) for branching, plate and massive corals, respectively (Appendix S1). The presence of spatial auto-correlation is explained by the mechanisms of coral recruitment that are related to the supply of larvae from plankton, suitability of substrate for coral settlement and mortality post-settlement (Connell et al., 1997). Among these factors, only the supply of larvae from plankton has the potential to act at the kilometre scale in conjunction with the interaction between habitat and currents that drive the number of new recruits in these areas (Tebbett et al., 2022). Connell et al. (1997) and Tanner (2017) suggested that the supply of plankton is likely to be higher on the southern slope of Heron Reef due to the proximity to other reefs, which increases coral recovery rates. However, we found that branching corals drove the recovery on the south slope and plate corals on the north slope. Further investigations will focus on the interactions between branching and plate corals within habitats to better understand the influences of connectivity, demographic traits of coral forms and competition for space in driving recovery patterns. For example, it is unclear if the recovery of branching corals didn’t occur in the northern slope during the surveyed years due to the growth of plate corals or because of something else.

Data-driven approaches to guide where and when to sample monitoring locations are applied to coral reefs (Kang et al., 2016; Mellin et al., 2020; Abeysiri Wickrama Liyanaarachchige et al., 2022). The quantification of spatial autocorrelation is informative for the design of coral reef monitoring because it quantifies the similarity of collected information between two locations (Hamylton, 2013). By extracting spatio-temporal structures of Heron Survey data, our results revealed that monitoring locations separated by 1 km and 1.5 km are pseudo-replicated observations for branching and plate corals, respectively. The presence of redundant information in monitoring data violates the assumption of independence between observations in traditional statistical tests, which bias inferences and ecological interpretations (Ver Hoef et al., 2018). We recommend that future designs of monitoring programs should ensure that surveys include locations both within and between a radius of 1.5 km. This important aspect will allow for collecting both replicated and spatially independent information, thereby optimizing our understanding of underlying mechanisms that drive coral dynamics. Also, monitoring locations should be sampled across different habitats, especially in more than one flank of the reef slope. In this way, surveys can provide enough ecological and spatial information about recovery patterns of the entire coral community. For example, without observations in the southern slope of Heron Reef, the lack of recovery of branching corals in the northern slope could have been generalized at the reef scale (and maybe region) whereas they have grown back in other reef flanks. Incorporating these additional aspects of reef data are key to capturing fine-scale variability of coral dynamics throughout the reef.

Scaling-up detection of spatial recovery

Disentangling the influence of space and time on coral recovery showcases different recovery scenarios across habitat and coral morphology (Figure 6). Branching corals successfully recovered in the southern slope, mostly due to high and fast growth in locations that were previously abundant. However, they didn't recover in the northern slope due a lack of growth. Plate corals flourished in the northern slope due to high growth, despite a large decline and medium-low baseline cover. They also recovered in the southern slope but in this case there was both a low decline and baseline. These complex scenarios highlight the fine-scale variability of coral dynamics, where recovery patterns of reef locations separated by small distances (only a hundred metres in this study) can be driven by different variables. Not considering this variation by, for example, averaging values across monitoring locations, contributes to uncertainty when estimating patterns at broader spatial scales. Our spatio-temporal model captures heterogeneous coral dynamics from three model parameters only, namely: spatial autocorrelation; range and variance; and temporal autocorrelation (Appendix S1). These parameters are used to estimate coral cover at predictive locations, along with other model parameters including habitat. Predictions are summarized via posterior distributions, which are key to propagating uncertainty across spatial scales. This bottom-up approach facilites consideration of heterogeneous fine-scale interplay between decline, growth, and baseline. It also enables prediction of patterns of recovery from finer to broader scales while propagating uncertainty appropriately. In this study, we used this method to model patterns of recovery from sub-site to the habitat scale.

We acknowledge that the high volume of data required to fully exploit the benefits of spatio-temporal statistical models is a limitation to their widespread adoption. Additional work is needed to estimate the minimum amount of data that will enable the implementation of spatio-temporal models to more than one reef. New coral-reef monitoring techniques, including the use of machine learning (González-Rivero et al., 2020), citizen science (Santos-Fernandez et al., 2021) and combined approaches (Peterson et al., 2020) to boost collection, processing and open access of reef data are rapidly being adopted by research and governmental institutions across the Indo-Pacific. Another limitation is the need for high computing power to employ complex Bayesian statistical models. Exciting advancements in statistical ecology that aim to address these challenges include the use of deep learning (Wikle and Zammit-Mangion, 2022) and a hybrid modelling framework (Sainsbury-Dale et al., 2021) to speed up estimation of the spatio-temporal structure from data. These advancements will allow models to include more detailed interactions between coral communities and to be scaled up to additional reefs and regions.

Conclusion

Assessment of coral recovery at large spatial scales is the first step to monitoring the efficiency of management actions (Anthony et al., 2020). The fine-scale variability of coral dynamics can contribute to increasing uncertainty and mask positive or negative changes in recovery patterns. In their recent review, Dornelas et al. (2023) call for increased recognition of the variability in biodiversity changes across space and time and identification of blind spots in our knowledge. This study contributes to this dialogue by showing that the fine-scale interplay between coral growth and decline drove recovery patterns of branching and plate corals at Heron Reef. Despite being variable, fine-scale coral dynamics are well-captured by spatio-temporal random effects, allowing propagation of uncertainty across spatial scales and estimation of recovery patterns at the habitat scale. This bottom-up approach can be further extended to identifying recovery at the scale of a reef and beyond, enabling characterization of representative recovery patterns at management scales. In this way, complex fine-scale coral dynamics can be considered when assessing recovery at large spatial scales, and the associated uncertainty can be viewed as indicator of the current state of knowledge. The integration of this concept into global assessment of reef recovery will therefore give equal weight to reefs and regions with different disturbance regimes.

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Author contributions

JV, CR, EK, MGR, ML and KM designed the study, JV, CR, EK and MGR processed the data, JV, MM and ML developed the spatio-temporal model. JV wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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Figure captions

Figure 1: Locations of Heron Reef, observations and spatial predictions. a) Locations of Heron Reef in the Great Barrier Reef, Queensland, Australia. b) Dots show the locations of surveyed 100m sub-sites across Heron Island Reef and habitats c) Predictive locations used in the spatio-temporal model. The boxed area indicates the area used to interpret the metrics of coral recovery.

Figure 2: Long-term trajectories of cover estimated by the model at the habitat scale for a) branching, b) plate, and c) massive corals. The dots and error bars denote the observed values and associated 95 % confidence intervals under the assumption of a normal distribution. The line and shaded areas are the model estimates showing the mean and 95% credible intervals estimated from the model posterior distributions. Note that the y-axis is on a different scale for the massive corals in panel c.

Figure 3: Metrics developed to characterize coral recovery by habitat and coral growth morphology. a) Probability of recovery changes through time for branching corals, b) Associated coral growth, c) Probability of recovery changes for plate corals and d) Plate growth at the habitat scale. Note that coral growth is expressed as a percentage.

Figure 4: Fine-scale characterization of successful recovery for branching corals.

a) Predictive locations on the reef slopes where branching corals recovered between 2008-2018, distributions of b) cover baseline, c) coral decline and d) coral growth by habitat.

Figure 5: Fine-scale characterization of successful recovery for plate corals. a) Predictive locations on the reef slopes where plate corals recovered between 2008-2018, distributions of b) cover baseline, c) coral decline and d) coral growth by habitat.

Figure 6: Visualisation of the four scenarios (two habitats and coral growth morphology) of recovery patterns characterized at Heron Reef. Symbols represent values of growth as a function of probability of recovery and decline for each recovery year. Bigger symbols indicate the first year of recovery. The horizontal dotted line shows the threshold used to determine successful recovery. Grey stars denotes minimum coral growth values associated with successful recovery.

Figures

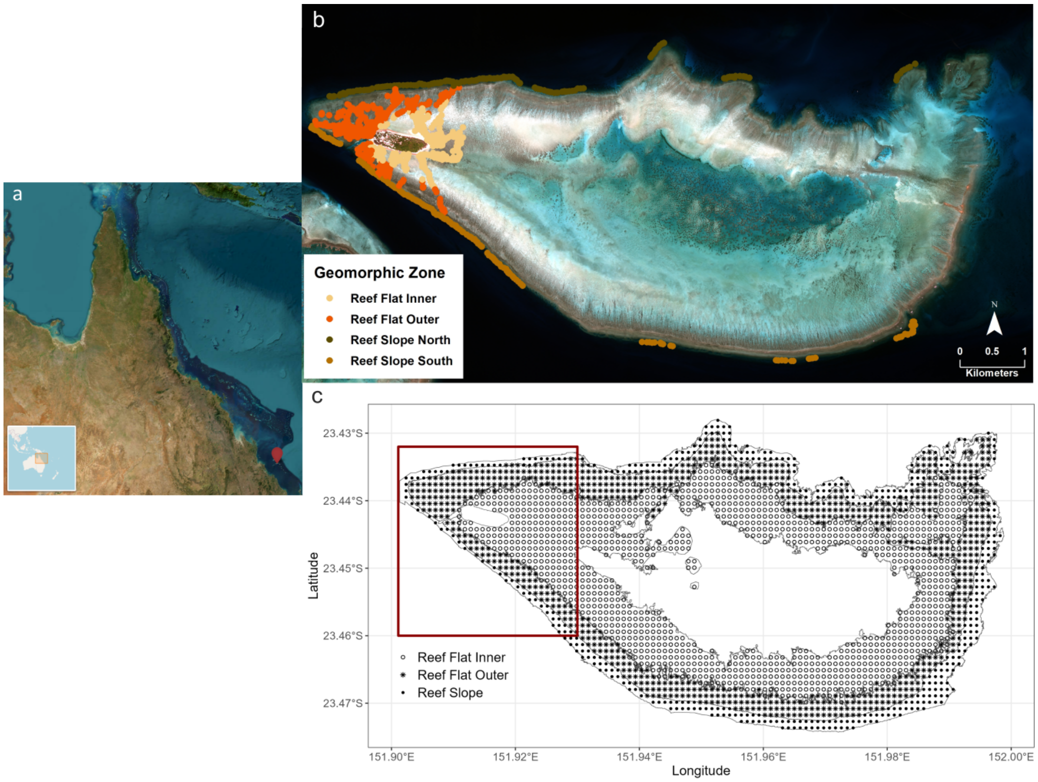
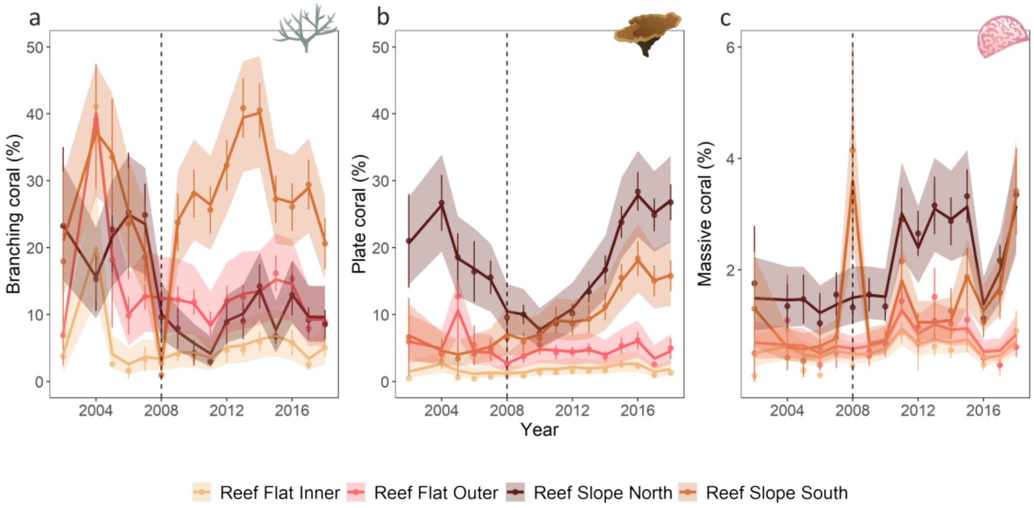


Figure 1



a
b
c
Branching coral (%)
Plate coral (%)
Massive coral (%)
0
10
20
30
40
50
0
2
4
6
2004
2008
2012
2016
Year
Reef Flat Inner
Reef Flat Outer
Reef Slope North
Reef Slope South

Figure 2

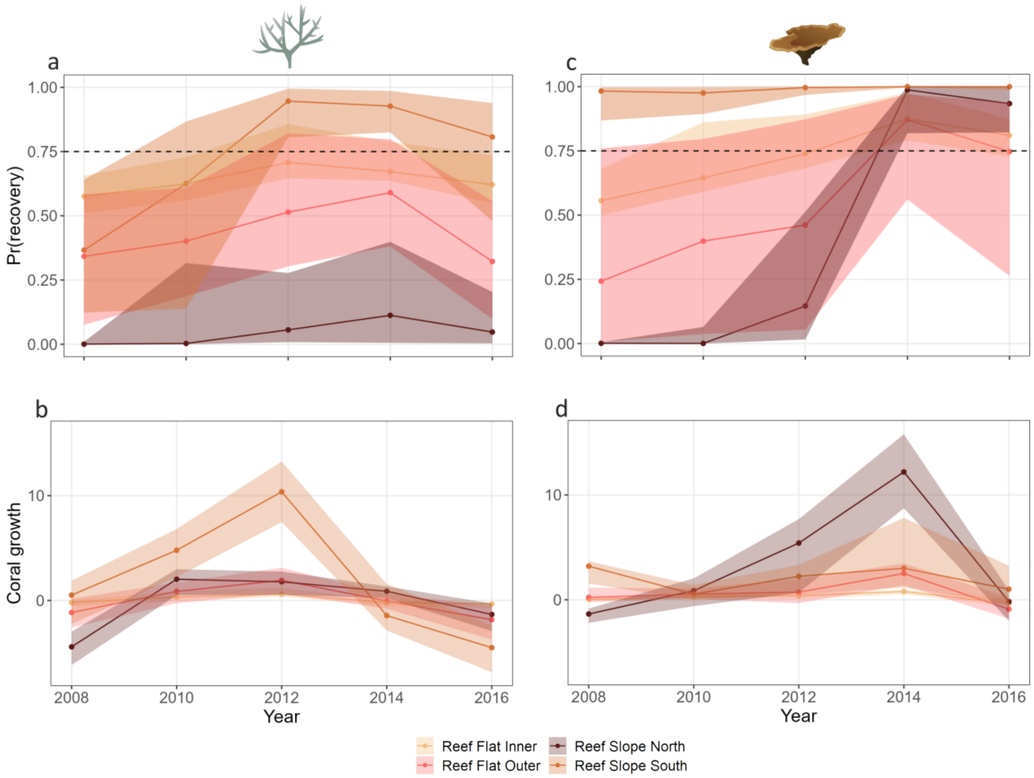

a
b
c
d
Pr(recovery)
1.00
0.75
0.50
0.25
0.00
Coral growth
10
0
2008
2010
2012
2014
2016
Year
Reef Flat Inner
Reef Flat Outer
Reef Slope North
Reef Slope South

Figure 3

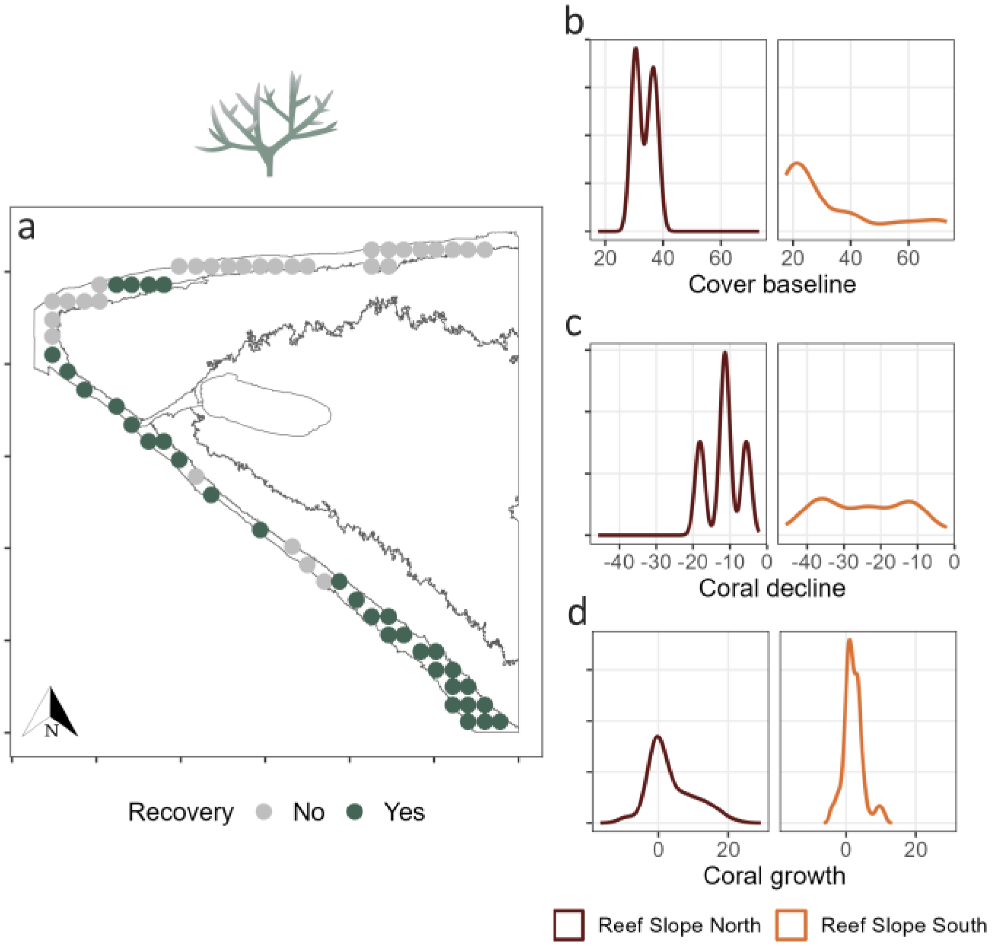

a
N
Recovery
● No
● Yes
b
20
40
60
20
40
60
Cover baseline
c
-40 -30 -20 -10 0
-40 -30 -20 -10 0
Coral decline
d
0
20
0
20
Coral growth
☐ Reef Slope North
☐ Reef Slope South

Figure 4

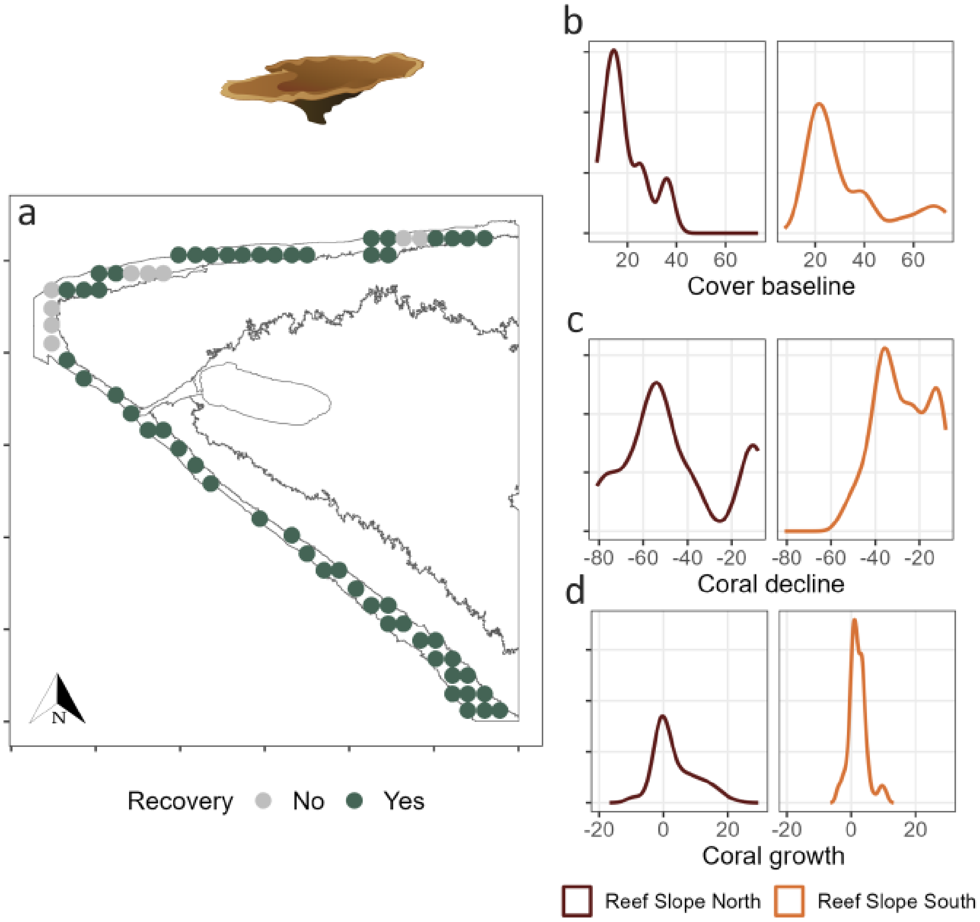

a
N
Recovery ● No ● Yes
b
20 40 60
20 40 60
Cover baseline
c
-80 -60 -40 -20
-80 -60 -40 -20
Coral decline
d
-20 0 20
-20 0 20
Coral growth
Reef Slope North
Reef Slope South

Figure 5

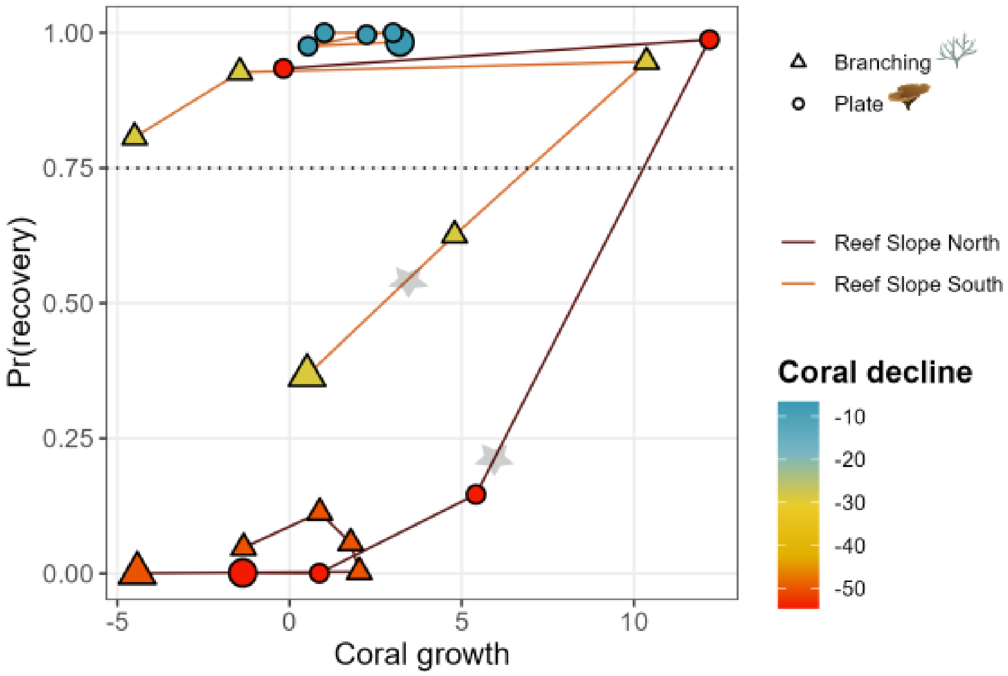

1.00
0.75
0.50
0.25
0.00
Pr(recovery)
-5
0
5
10
Coral growth
Branching
Plate
Reef Slope North
Reef Slope South
Coral decline
-10
-20
-30
-40
-50

Figure 6