Research article

Maximising the benefits of local management for coral reefs amidst near-term environmental change

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ABSTRACT

Pest species cause significant ecological and economic damage globally. The Crown-of-Thorns starfish (CoTS; *Acanthaster* spp) drives coral mortality across the Indo-Pacific, including on the Great Barrier Reef (GBR), where cyclones and bleaching also threaten coral. Manual CoTS control mitigates coral loss, but the factors driving control efficacy amidst environmental change remain uncertain. Using a spatially explicit ecosystem model of the GBR to simulate past, current, and future CoTS outbreaks (2008–2040), we compared coral cover between "CoTS control" and "no control" scenarios, and explored how control, disturbances, and ecological variables influenced outcomes. CoTS control generated cover benefits in 84.5 % of predictions, with a third of controlled reefs achieving >10 % cover gains. Benefits also increased over time. Cover deficits (15.5 %) were rare relative to benefits and generally small (<10 %). Reefs were more likely to experience benefits with increasing proportions of CoTS-preferred coral prey, frequency of control, and period between disturbances. High CoTS densities and larval supply and frequent disturbances reduced cover benefits, while rubble, coral larval supply, and control recency had limited effects. There were differences between reefs based on their geographic region, and whether they were targeted for control, with more pronounced benefits on reefs targeted for control and reefs in the north. Our results clearly demonstrate that CoTS control can generate substantial, and increasing, coral cover benefits at many reefs across the GBR to 2040, even under future climate change trajectories and, for the first time, identifies which factors contribute to the greatest cover benefits from control.

1. Introduction

Pest species, whether native or alien, cause substantial ecological and economic damage to terrestrial and aquatic systems worldwide (Levins and Wilson, 1980; Kogan, 1998). Integrated pest management, which leverages pest biology, environmental information, and new technology, is a holistic and science-based practice that is used to control populations sustainably (Brewer and Goodell, 2012; Dara, 2019). While sustainable pest control is prevalent in terrestrial and agricultural systems (e.g., Kross et al., 2016), managing pests in aquatic ecosystems poses additional and inherent challenges due to the enhanced connectivity from the flow of water (Goldson et al., 2015). Finding natural solutions that have a minimal impact on the surrounding environment is therefore difficult (Hubert et al., 2019). One example of integrated pest management in the aquatic realm involves control of the corallivorous Crown-of-Thorns Starfish (CoTS; *Acanthaster* spp) (Westcott et al., 2016;

Fletcher et al., 2020). Although native to the Indo-Pacific, their populations exhibit classic boom-and-bust dynamics with extreme fluctuations in densities (Uthicke et al., 2009; Deaker and Byrne, 2022). When CoTS populations reach outbreaking densities, they can cause widespread coral mortality on reefs throughout the region (Dulvy et al., 2004; Timmers et al., 2012; Yasuda, 2018; Reimer et al., 2019). Direct control, through either manual removal or injection with household vinegar that kills individuals in situ (Boström-Einarsson and Rivera-Posada, 2016), has proven to be effective at reducing CoTS populations below levels that are harmful for coral communities, although continued efforts are required given the length and persistence of their outbreaks (Pratchett et al., 2014).

On the Great Barrier Reef (GBR), successive cyclones, temperature-induced bleaching events, and outbreaks of predatory CoTS, are responsible for substantially reducing hard coral populations (De'ath et al., 2012; Bozec et al., 2022; Emslie et al., 2024a). While climate

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change and extreme weather events are hard to manage locally, CoTS populations can be directly managed through targeted culling (Babcock et al., 2016). The CoTS Control Program, initiated in 2013 (Westcott et al., 2016) and fully implementing an IPM framework from 2019 (Fletcher et al., 2020) under the leadership of the GBR Marine Park Authority (GBRMPA), has proven to be effective at mitigating CoTS populations and increasing coral cover across the GBR Marine Park (Babcock et al., 2020; Westcott et al., 2020; Castro-Sanguino et al., 2023; Rogers et al., 2023; Matthews et al., 2024). However, while the ecological benefits of CoTS control on the GBR are increasingly recognised, there is likely to be substantial variability in how individual reefs respond to CoTS culling due to a myriad of spatial and temporal factors. For example, the benefits of CoTS control on coral populations may be significantly reduced where reefs are subsequently subjected to other stressors or disturbances, such as coral bleaching and cyclones (Rogers and Plagányi, 2022). It can also be difficult to distinguish how much of the coral cover increase is directly due to CoTS control efforts versus how much results from natural recovery processes, such as coral recruitment and growth, that occur independently of management interventions. Given the considerable variability in coral community dynamics across the GBR, coupled with the substantial operating costs of the CoTS Control Program (Fletcher et al., 2020) and the intensifying regime of climate-driven disturbances (Hughes et al., 2017; Oliver et al., 2018; Emslie et al., 2024b), it is crucial to discern the mechanisms that lead to sustained benefits from targeted control efforts amidst environmental change. However, achieving a robust assessment of these benefits necessitates evaluating them against systematic controlled conditions (i.e., no culling of CoTS for the same environmental context and disturbance), a challenge that is difficult to operationalise effectively in the field.

Here, using a spatially explicit ecosystem model of the Great Barrier Reef as a case study, we simulate the ecological impacts of targeted local action against CoTS across >3,000 individual reefs under their recent and near-term future regime of climate-driven disturbances, represented by three separate global climate models (GCMs), and identify key factors influencing management success. In this model experiment, for each GCM, we measure management outcomes by comparing the difference in coral cover percentage points (%) between a CoTS control scenario and a baseline scenario without CoTS control, with positive cover changes considered cover benefits and negative cover changes considered cover deficits. Specifically, over the near term (2019–2040), we ask: 1) What is the magnitude of coral cover differences from CoTS control at each reef? 2) What happens after control stops at a reef, and how quickly do changes occur? 3) How do natural disturbances (i.e., bleaching and cyclones) influence coral cover differences? 4) What other conditions or mechanisms affect coral cover benefits or deficits? Identifying these factors will contribute to more effective CoTS control practices, supporting reef resilience in the face of environmental change.

2. Materials and methods

2.1. Ecosystem model: ReefMod-GBR

ReefMod-GBR (Mumby, 2006; Bozec et al., 2022) is a spatially explicit ecosystem model that simulates coral and CoTS population dynamics across the extent of the Great Barrier Reef (~2300 km) (Fig. 1) in MATLAB 2021b (The MathWorks Inc, 2021). The model is described in detail in Bozec et al. (2022) and Castro-Sanguino et al. (2023), so is only explained briefly here (see Table S1 for all parameters). There are 3806 reefs, each being modelled using a 20 × 20 m (400 m²) representative seascape that can be colonised by individual coral colonies and CoTS. Corals belong to six morphological groups (acroporids: arborescent, plating, corymbose; non-acroporids: pocilloporids, encrusting/submassive, large massive).

Demographic processes, such as settlement, reproduction, and mortality, drive the dynamics of coral community and CoTS populations on

every reef in six-month timesteps (Bozec et al., 2022). Broadcast coral spawning occurs on the GBR from October to December (Babcock et al., 1986), with fecundity based on colony size and reproductive output volume (Hall and Hughes, 1996). CoTS spawning occurs from December to February, with fecundity determined by wet mass and age (Kettle and Lucas, 1987), and sexual maturity reached at two years (Lucas, 1984). For recruitment, the total incoming coral and CoTS larvae are divided by individual reef area to estimate larval density (larva/m²). Settlement potential is then modelled using a Beverton-Holt function (Haddon, 2011) to account for early density-dependent survival. For CoTS, settler densities are reduced to 3 % survival due to predation (Keesing and Halford, 1992), while coral recruits are simulated separately for each group using a Poisson distribution, with recruitment rates proportional to available settlement space. Inter-reef larval connectivity is derived from simulated particle dispersal using the eReefs hydrodynamic model (Hock et al., 2014, 2017, 2019; Steven et al., 2019). CoTS larvae rely on phytoplankton availability on inshore reefs, so total chlorophyll a concentrations predicted by eReefs enhance their survival (Fabricius et al., 2010; Wolfe et al., 2017). Demographic outcomes are scaled to the actual size of the reef rather than the grid.

CoTS outbreak dynamics are simulated by structuring starfish into 6-month age classes and subjecting individuals to reproduction, chlorophyll-limited larval survivorship, food availability, and age-specific mortality (Bozec et al., 2022). Age-specific CoTS mortality rates were initially sourced from the literature and calibrated to a hindcast time series of 3 years of CoTS density from Lizard Island (Pratchett, 2005). As Lizard Island is protected from fishing, we reduced age-specific CoTS mortality rates to reflect lower mortality rates for CoTS on reefs in fished zones (Kroon et al., 2021). With a reduction factor of 0.76 applied to all mortality-at-age classes, the demographic model reproduces the increase of adult CoTS density observed in fished zones compared to protected zones (Skinner et al., 2024). Reefs are assigned a status of protected (e.g., Green and Pink zones) or unprotected consistent with the GBR Marine Park Authority (unpublished data).

CoTS densities are simulated as individuals per 400 m² grid but converted to "CoTS per tow" for comparison with the manta tow monitoring method (Miller et al., 2003). Developed by the Australian Institute of Marine Science (AIMS), manta tow is a standardised monitoring technique used in the Long-Term Monitoring Program (LTMP) to estimate coral cover and CoTS densities across large reef areas. During each 2-min tow, a diver is towed behind a vessel at a speed covering ~200 m, with a 5-m detection width on either side (Miller et al., 2003). Although manta tow has relatively low accuracy, it achieves reasonable precision through repeated measurements. Due to the extensive use of manta tow data, reef management thresholds are often reported in "CoTS per tow" units. For example, GBRMPA defines an outbreak when the average density exceeds 0.22 CoTS per tow across all tows around a reef's perimeter (Matthews et al., 2024). To convert CoTS densities from the 400 m² grid to CoTS per tow, each CoTS age class density is first corrected for imperfect detectability using empirical predictions from MacNeil et al. (2016). The values are then converted, assuming that 0.22 CoTS per tow is equivalent to 1500 CoTS per km² (Moran and De'ath, 1992), then 1 CoTS per grid (400 m²) is equivalent to 0.22*2500/1500 (Bozec et al., 2022).

On a reef, an outbreaking population of CoTS (i.e., CoTS density >0.22 per tow) collapses and resets to background levels either after starvation (when the total cover of preferential coral prey falls below 5 %) or once reef-level outbreaking densities have persisted for more than 2–5 years (number randomly drawn) (Moran, 1986; Zann et al., 1987, 1990). Background levels were determined by analysing CoTS observations from the AIMS LTMP (see Castro-Sanguino et al., 2023). On most reefs this was ~0.004 CoTS/tow (or 0.01 CoTS per 400 m² grid). For reefs in the "initiation box", a speculative area of primary outbreaks on the GBR (≤ −14.6 and ≥ −17 latitude; Moore, 1990; Pratchett et al., 2014), it was set to ~0.04 CoTS/tow (or 0.1 CoTS per 400 m² grid),

Fig. 1. The Great Barrier Reef off the coast of Queensland, Australia, with the four management zones delineated by the Great Barrier Reef Marine Park Authority (GBRMPA). Although reefs located north of the Far North region fall outside the official management zone, they are included in the model as part of this region for simulation purposes.

based on the assumption that the emergence of CoTS outbreaks in this region may be partly explained by higher background densities (Moore, 1990). The full parameterisation and calibration of CoTS dynamics is detailed in Bozec et al. (2022) and Castro-Sanguino et al. (2023).

For coral, individual reefs are initialised in 2008 with coral cover data from the AIMS LTMP and community composition data from 214 reefs (Sweatman et al., 1998). Predictions of coral cover from 2009 to 2018 show high congruence with observations at 67 LTMP sites (Bozec et al., 2022), although coral cover observations are not used to reset predictions, even if substantial deviations occur. For CoTS, individual reefs are initialised with adult CoTS density hindcast predictions from the Coral and CoTS network metacommunity model (CoCoNet), which have been tested against LTMP CoTS data (Condie et al., 2018). Where data are available, the CoTS model in ReefMod is updated with manta tow survey observations from the CoTS Control Program (CP), Field Management Program (FMP), and LTMP, which override model predictions at individual reefs and years.

2.1.1. Disturbances

Corals are also affected by environmental pressures such as heat stress, cyclones, and water quality that vary across locations and years. The model's hindcast, covering 2008–2022, uses spatially and temporally-explicit data about disturbance exposure data, and reconstructs the impacts of those multiple stressors on coral cover (Bozec et al., 2022). We extended the hindcast with stochastic disturbance events to project coral cover and CoTS until 2040 to assess the impacts of disturbances and CoTS control over a longer period, while still focusing on the near term (i.e., <2040; The Intergovernmental Panel on Climate Change (IPCC), 2023). Projections were not extended beyond 2040 due to the increasing uncertainty associated with predicting conditions over longer timescales (i.e., long term; IPCC, 2023; Bozec et al., 2025). Future heat stress regimes were based on daily temperature projections from three distinct CMIP6 GCMs: 1) CNRM-ESM2-1 (Séférian et al., 2019), 2) MIROC-ES2L (Hajima et al., 2020), and 3) MRI-ESM2-0 (Yukimoto et al., 2019). All models were run under the Shared Socioeconomic Pathway (SSP) emissions scenario SSP1-2.6, which represents a pathway of moderate global CO_2 emissions reduction by the end of the century. Although driven by the same scenario, these models produce divergent warming trajectories, allowing us to capture a broader range of plausible future climate conditions and associated ecological responses. Other SSP scenarios were not included, as projected warming trajectories, and the corresponding coral cover on the GBR, remain relatively similar across scenarios until around 2040 (Bozec et al., 2025), with greater divergence emerging only in the second half of the century.

The severity of coral bleaching from accumulated temperature stress was determined using the Degree Heating Week metric (DHW, °C-weeks), which represents the number of weeks in which sea surface temperatures exceed the maximum monthly mean by 1 °C (Gleeson and Strong, 1995). Future cyclone regimes were based on synthetic cyclone tracks for the GBR (Wolff et al., 2016), while future water quality was represented by randomly selecting hindcast spatial layers of suspended sediments from eReefs (Steven et al., 2019). Coral mortality from these disturbances produces loose debris, known as coral rubble (Wolfe et al., 2021; Kenyon et al., 2023). The amount of rubble generated corresponds to the percentage of coral lost. While this process occurs immediately following cyclones, it is delayed by three years after bleaching events or CoTS predation (Sano et al., 1987). As coral juveniles do not survive on unconsolidated rubble, their survivorship is reduced by the proportion of the reef area covered by rubble (Fox et al., 2003). Coral rubble stabilises over time, with two thirds of rubble consolidated after four years (Biggs, 2013).

2.1.2. CoTS control program

The GBR CoTS Control Program (CCP) was simulated from 2019 onwards, following Castro-Sanguino et al. (2023) and Skinner et al. (2024). The goal of the CCP is to reduce CoTS densities below the

ecological threshold (ET; Babcock et al., 2014), where the rate of coral growth is higher than the rate of CoTS consumption (0.04 CoTS/min at < 40 % coral cover). The GBRMPA identifies 500 priority reefs for CoTS control based on ecological, economic, and cultural values. Each year, a dynamic target reef list is generated from this to guide control activities. To simulate this, we created a fixed target reef list (n = 224) by selecting all priority reefs that were controlled at least twice over a three-year period ('21/22, 22/23, and 23/24; GBRMPA, unpublished data). Each reef was split into 10-ha cull sites (500 × 200 m), and control was implemented at this level when CoTS were above the ET. The number of cull sites for a reef was determined as follows; 1) Existing Data: If the number of cull sites for a reef was already available (GBRMPA, unpublished data), this value was used. 2) No Existing Data: If the number of cull sites was not available, a linear regression model based on the Control Program data and the Reference Area was applied. The Reference Area represents the 2D area (km^2) of the reef polygons used by the GBRMPA, which considers a total area of 24,776.37 km^2 for all 3806 reefs. The equation for the fit is:

$$NumberOfCullSites = 12.13 + 0.77*ReferenceArea$$

with an R^2_{adj} of 0.69. This was rounded to the nearest integer, totalling 64,944 cull sites for all reefs.

At each timestep, control began at target reefs, then priority reefs, then non-priority reefs until all culling effort was used. Within each simulation run, a consistent randomisation was maintained so that the order of reef visitation was the same at each timestep. The total effort for control activities across the GBR was calculated as 19,200 h (3840 h per vessel per year x 5 vessels). However, current CCP data (GBRMPA, unpublished data) suggests that ~10 % of total effort is spent on other on-water activities such as manta tow surveys, leaving 90 % of total effort allocated to culling, or 17,280 h (3456 h of culling effort per vessel per year x 5 vessels).

2.2. Data analysis

2.2.1. Coral cover differences from CoTS control

For each GCM, two scenarios were run from 2008 to 2040: 1) a counterfactual with no CoTS control, and 2) a CoTS control scenario with culling implemented from 2019 as detailed above. Since most of the implemented processes are stochastic at the colony or reef level, the model is run multiple times using different sequences of random numbers to capture the variability of the simulated demographics and disturbance exposure (Bozec et al., 2022). Here, a scenario was run 20 times (i.e., 20 repeated runs) by varying the seed that initialises the generation of random numbers. The same 20 seeds were used for both scenarios to ensure a consistent stochastic scheme of cyclone and bleaching events. As the model runs on a seasonal (six-month) timestep, an annual mean was calculated for all variables across summer and winter seasons. To assess potential impacts of CoTS control, the difference in coral cover between CoTS control and the counterfactual scenario was calculated for each GCM/reef/year/run (hereafter, "cover difference (%)"). Coral cover differences were expressed as percentage points (i.e., absolute change) so 10 % coral cover in the CoTS control scenario vs. 5 % in the counterfactual for a given GCM/reef/year/run represents a 5 % cover benefit due to CoTS control.

Cover differences were assessed for four reef groups: 1) controlled reefs where direct CoTS control was implemented; 2) uncontrolled reefs identified as CoTS sinks; 3) uncontrolled reefs identified as coral sinks; and 4) uncontrolled reefs that were neither controlled nor identified as sinks. Key sink reefs were identified by averaging connectivity matrices for CoTS and coral, respectively, across all years to detect persistent patterns in larval supply, accounting for the time lag between larval settlement and observable changes in coral cover. For CoTS, key sinks were defined as reefs receiving ≥5 % of their larval input from a controlled reef, while for corals, the threshold was ≥2.5 %. The lower

threshold for corals reflects their typically more localised dispersal and shorter larval survival (Ayre and Hughes, 2000; Jones et al., 2009) compared to CoTS larvae, which are longer-lived, more dispersive, and can be transported farther by currents (Uthicke et al., 2015; Pratchett et al., 2017), resulting in a greater number of potential connections. Reef classification was dynamic: reefs were included as controlled from their first control event, as sinks from the first year they were linked to a controlled reef, and were excluded once they became impacted. Cover differences between these four reef groups were assessed with a linear mixed-effects model (lme4 R package; Bates et al., 2015); continuous cover difference was the response variable, reef group (controlled; uncontrolled CoTS sinks; uncontrolled coral sink; uncontrolled) was the predictor, and simulation run (i.e., 1–20) and GCM (i.e., CNRM-ESM2-1, MIROC-ES2L, and MRI-ESM2-0) were random effects.

While positive cover differences (e.g., benefits, where cover in the control scenario was larger than in the counterfactual) were more common, negative cover differences (e.g., deficits, where cover in the control scenario is less than in the counterfactual) can also emerge due to the stochastic nature of many ecological processes in the model (e.g., background mortality, coral settlement, and predation by CoTS). This is because each model run assigns a unique pseudo-random number seed, controlling the timing and magnitude of these events within two scenarios, the Counterfactual and CoTS control. Applying CoTS control alters the CoTS densities that the stochastically driven processes operate on, so that the exact same events cannot be replicated, resulting in delta differences (e.g., CoTS control minus Counterfactual) for selected outputs like coral cover. These differences, which can be positive or negative at the reef level, may represent random noise rather than clear ecological gains or losses, particularly when small. While averaging across runs typically reduces such fluctuations, each run here was kept separate as it follows its own unique disturbance and control trajectory. This approach acknowledges the individual variability due to the model's stochasticity, identifying the factors that drive cover differences in each scenario iteration. As such, disentangling random noise from consistent patterns in ecological processes is challenging (Grimm et al., 1996; Grimm and Railsback, 2012), particularly as a large proportion of cover differences fell between 0 and ±0.5 %. To focus on more substantial differences likely driven by the ecological impacts of CoTS control and to minimise the influence of random fluctuations inherent in the model, the analysis focused on cover differences of at least ±5 % (i.e., < −5 % or >5 %). Additional cover thresholds of ±0.5 % (i.e., < −0.5 % or >0.5 %) and ±10 % (i.e., < −10 % or >10 %) were also explored to test the sensitivity of the results.

2.2.2. Drivers of coral cover differences

Variables that might explain cover differences among reefs were extracted for each GCM/reef/year/run (Table 1). Many of the ecological predictor variables were expressed as deltas (the difference between the CoTS control scenario and the counterfactual (no control) scenario), since the aim was to explore how differences in these predictors drove changes in outcomes, rather than their absolute values within a single scenario. All numeric predictors were scaled and centred and multicollinearity was assessed by calculating the Variance Inflation Factor (VIF) through a stepwise procedure (usdm R package; Naimi et al., 2014) with a conservative theta = 3. No variables were removed through this process. Three global non-linear mixed effects models (NLME) (nlme R package; Pinheiro et al., 2023) were built with the cover difference threshold group (±0.5 %, ±5 %, ±10 %) as the response variable, and all variables as fixed predictors. Simulation run (i.e., 1–20) and GCM (i.e., CNRM-ESM2-1, MIROC-ES2L, and MRI-ESM2-0) were included as crossed random effects. All possible NLME models were compared with all combinations of fixed effects (MuMIn R package; Bartoń, 2023), with model selection based on AICc. For the ±0.5 % and ±5 % threshold models, no other models were within 2 AICc units of the top models, which were therefore clearly identified as the best-supported models. For the ±10 % threshold model,

Table 1

Extracted predictors of coral cover differences for each GCM/reef/year/run. The asterisk (*) indicates a lagged predictor - as coral cover is a long-term lagged variable, it may be influenced by multiple preceding years for some predictors. Delta (Δ) indicates the difference between the CoTS control scenario and the counterfactual scenario with no CoTS control.

Predictor	Detail	Rationale
Control Frequency	Total number of control events prior to that year.	A reef that is controlled more regularly may sustain greater benefits.
Coral Habitat Area	The mapped 3D area (km²) of coral habitat for an individual reef (Roelfsema et al., 2021).	Coral cover differences may depend on the extent of available coral habitat, as larger or more complex habitats can be more challenging to manage and control, potentially affecting recovery rates and the effectiveness of interventions.
Coral Larval Supply*	Δ geometric mean of the coral larval supply (i.e., combined external supply and self-supply) to a reef over the previous 5 years.	A 5-year geometric mean of the Δ of coral larval supply (both external and internal) is used to capture the long-term trends in larval recruitment and accumulation. This longer duration not only accounts for multiple recruitment events showing how sustained larval supply affects coral recover, but also the slower recovery process of corals (Johns et al., 2014; Sato et al., 2018; Gouezo et al., 2021).
CoTS Density*	Δ geometric mean CoTS per manta tow at a reef over the previous 3 years.	The density of CoTS will determine the extent of their influence on coral cover differences. A 3-year geometric mean of the Δ was used because CoTS larvae, once settled, take approximately 2 years (Pratchett et al., 2014) to reach a detectable size (MacNeil et al., 2016), allowing for an accumulation of individuals.
CoTS Larval Supply*	Δ geometric mean of the CoTS larval supply to a reef over the previous 3 years.	A 3-year geometric mean of the Δ of CoTS larval supply was used to capture the long-term trends in larval recruitment and accumulation, as CoTS take approximately 2 years once settled to reach a detectable size (Pratchett et al., 2014; MacNeil et al., 2016). This duration accounts for multiple recruitment events showing how sustained larval supply contributes to CoTS outbreaks over time.
CoTS-Preferred Coral Prey*	Δ mean proportion of coral acroporids and pocilloporids (preferred CoTS coral prey) on a reef over the previous 3 years.	Different coral taxa respond differently to disturbances (Darling et al., 2013) and CoTS populations may fluctuate with food availability (Pratchett et al., 2014), impacting coral cover differences. A 3-year mean of the Δ smooths out annual variability, providing a more stable representation of the community dynamics which might influence coral cover outcomes.
Disturbance Frequency	Cumulative total number of disturbance events prior to that time point (since 2008). A disturbance here is defined as a cyclone category (Saffir-	Reefs subjected to frequent disturbances may struggle to retain management benefits.

Table 1 (*continued*)

Predictor	Detail	Rationale
	Simpson scale) ≥ 3 and Degree Heating Week ≥ 6 °C-week.	
Reef Type	Target, priority, or non-priority.	Control is implemented first at target reefs, then priority, and then non-priority reefs, with target and priority reefs often chosen based on their ecological or economic value. The order of prioritisation may influence coral cover outcomes.
Region	Far North, North, Central, South.	Coral and CoTS populations may vary spatially due to differing environmental features and habitat. See Fig. 1 for the regions. Although reefs located north of the Far North region fall outside the official management zone, they are included in the model as part of this region for simulation purposes.
Rubble Cover*	Δ mean percent cover (%) of rubble on a reef over the previous 3 years.	Rubble cover, resulting from coral degradation after disturbances, indicates long-term impacts on reef health and potential influences on coral cover recovery. A 3-year mean of the Δ was taken as structural collapse occurs immediately after cyclones but is delayed for up to three years following bleaching and CoTS predation (Sano et al., 1987).
Years Since Control	Number of years since CoTS control was last implemented.	A reef that is controlled more recently may experience greater cover benefits.
Years Since Disturbance	Number of years since a disturbance event. A disturbance here is defined as a cyclone category ≥ 3 and Degree Heating Week ≥ 6.	A reef experiencing recent disturbances may lose cover benefits.

one additional model was within 2 AICc units of the top-ranked model. However, the top model held a dominant Akaike weight (0.7), indicating substantially stronger support, and was therefore selected as the top model. All model residuals were plotted and checked to confirm model assumptions were met. For each model, the importance of the predictors was based on the size of the effect on cover differences rather than the statistical significance, as it is inappropriate and uninformative to interpret outputs from simulation models using p-values (White et al. 2014). The predictors with the largest effect sizes were plotted against the response. All analyses were conducted in R 4.3.1 (R Core Team, 2023).

3. Results

The counterfactual scenario with no CoTS control revealed consistent coral decline across all GCMs examined (Fig. 2a). All three models projected substantial reductions in mean coral cover from approximately 25 % in 2020, with MIROC-ES2L showing the most severe decline to around 5 % by 2030, while CNRM-ESM2-1 and MRI-ESM2-0 demonstrated more gradual trajectories ending at 12 % and 10 % respectively by 2040. Considerable uncertainty was evident across the 20 individual model runs (10th - 90th percentiles), with variability generally narrowing toward the end of the projection period, especially for MIROC-ES2L.

3.1. Coral cover differences from CoTS control

Across the three GCMs, and all reefs, years, and individual runs (n = 378,849 reef-level predictions), mean ($\pm$s.d.) coral cover differences on controlled reefs were low (1.28 $\pm$ 3.63 %), but the range in values was large (min = −35.71 %; max = 68.23 %). The predicted cover differences were predominantly cover benefits (84.5 % of predictions >0.5 %) rather than cover deficits (15.5 % of predictions < −0.5 %) (Fig. 2b). For all three GCMs, coral cover benefits increased steadily from 2019 to 2040, with a growing number of reefs falling into higher benefit categories over time (Fig. 2b). This trend reflects the increasing number of reefs subjected to control (Fig. S1), and thus included in the analysis, as time went on. While coral cover deficits remained low and relatively consistent throughout the scenario periods, cover benefits continued to rise for CNRM-ESM2-1 and MRI-ESM2-0. In contrast, cover benefits under MIROC-ES2L plateaued after 2035, indicating a leveling off in the accumulation of cover gains in this scenario.

Of the 1,140 controlled reefs analysed over the scenario timeframes when considering all three GCMs, cover benefits were widespread. Nearly 40 % of controlled reefs exhibited gains in coral cover exceeding 5 %, with 30 % surpassing 10 %, 18 % exceeding 20 %, and 10 % achieving gains greater than 30 %. In contrast, cover deficits were less common: 15 % of controlled reefs experienced losses greater than 5 %, 7 % declined by more than 10 %, 1.5 % by more than 20 %, and just 0.3 % showed losses exceeding 30 % (Fig. 3).

Although predicted cover differences varied across the three GCMs, the distribution of controlled reefs remained consistent across reef types: most observations were from target reefs (53–76 %), followed by priority reefs (24–34 %) and non-priority reefs (0.3–13 %) (Fig. S1a). In contrast, the number of controlled reefs varied more across regions. For all three GCMs, the Northern region accounted for the largest proportion of controlled reefs (27–35 %). For CNRM-ESM2-1 and MIROC-ES2L, the next most controlled regions were the Central (25.5–29 %), South (23.5–25 %), and then the Far North (12–19.5 %). In contrast, MRI-ESM2-0 showed a more even distribution across regions, with the Far North (26.5 %) having the second highest number of controlled reefs, followed by the Central (24 %) and South (23 %) (Fig. S1b).

Cover differences were observed between reef groups across all three GCMs, with only slight variations between models (Fig. 3; Fig. S2). Controlled reefs consistently showed the highest proportion of cover benefits (>80 %), particularly in the higher cover categories, and few cover deficits (<20 %). Controlled reefs experienced significantly higher coral cover benefits than all other reef groups (p < 0.001), with the lowest benefits observed on uncontrolled reefs and CoTS sink reefs.

Coral sinks had significantly higher cover outcomes than CoTS sink reefs and completely uncontrolled reefs (p < 0.001), but still lower than controlled reefs. Differences in cover benefits and deficits across uncontrolled sink reefs and completely uncontrolled reefs were minimal in all three GCMs.

3.2. Drivers of cover differences on controlled reefs

The analysis primarily focused on cover differences of at least ± 5 % to better determine the more substantial ecological impacts of CoTS control. At this threshold (± 5 %), there were 28,202 model predictions across 485 unique reefs (12.75 % of all 3806 reefs) across the three GCMs and their 20 runs. However, cover differences at ± 0.5 % and ± 10 % thresholds were also explored to capture both small-scale and larger scale variations and examine the consistency of patterns in cover differences. At the lower threshold of ± 0.5 %, there were 175,722 model observations across 1002 reefs (26.3 % of all reefs), while at the ± 10 % threshold, there were 11,382 observations from 372 reefs (9.8 % of all reefs).

The best model explaining cover differences beyond < - 5 % and >5 % included all predictors (Table S2; Fig. 4). Half of the numerical predictors increased cover benefits, with a higher proportion of CoTS-
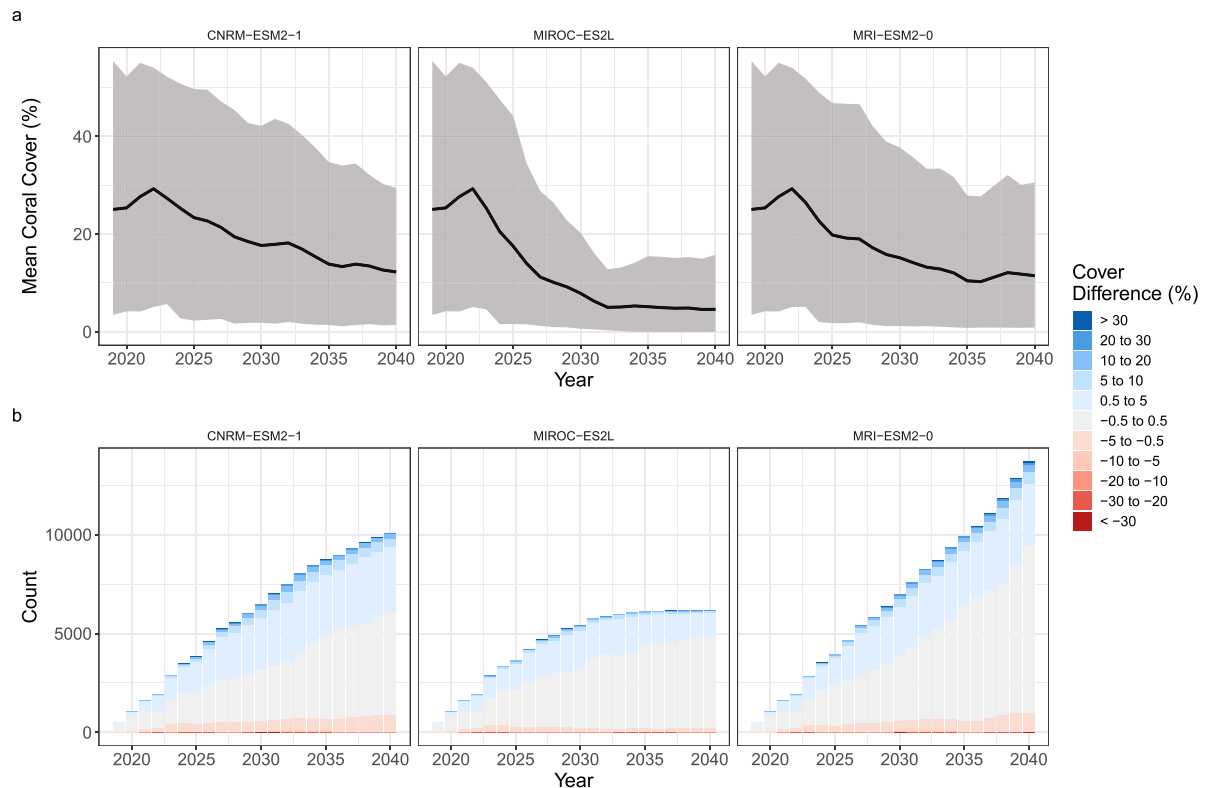
Fig. 2. a) Mean coral cover across all reefs in the counterfactual scenario with no CoTS control. Shaded ribbons indicate the 10th and 90th percentiles across 20 individual simulation runs for each scenario. **b**) Cover difference (%; coral cover scenario – coral cover counterfactual) for each controlled reef from 2019 to 2040, for all 20 pairs of stochastic runs of the three simulated climate scenarios. Cover differences are only for controlled reefs from the year that control first occurred.

preferred coral prey (e.g., Acroporids and Pocilloporids) in the coral community (Fig. 4d) having the largest positive effect (standardised coefficient 2.38). The time since the last disturbance (i.e., the recovery period) also increased cover benefits and reduced deficits, especially after ~10 disturbance-free years (Fig. 4h). Notably, substantial cover benefits were observed even immediately after disturbances, including cases where disturbances occurred within the same year. However, when disturbance frequency exceeded ~7 events, cover benefits declined, though fewer cover deficits were also recorded (Fig. 4e). Cover benefits also increased with more frequent control events, with cover deficits disappearing after approximately 15–20 control events (Fig. 4a). Cover deficits increased with higher CoTS densities (Fig. 4b) and CoTS larval supply (Fig. 4c), although a large proportion of both benefits and deficits occurred at a CoTS density and CoTS larval supply of 0. Coral habitat area, years since the last control event, coral larval supply, and rubble had weaker effects (Fig. S3). Coral habitat area and years since control had minor negative effects (standardised coefficient −0.4 and −0.39); the largest benefits and deficits appeared immediately post-control with effects tapering off after about ~5 years. Coral larval supply and rubble had minor positive effects (standardised coefficient 0.3 and 0.17). Cover differences also varied by region and reef type (Fig. 4f; Fig. 4g; Fig. 5). Compared to the central region (the intercept), all reefs exhibited more negative differences (FN: −0.55; N: −1.25; S: −1.4). Target and priority reefs also had more negative cover differences (−0.49 and −0.94, respectively) than non-priority reefs (the intercept) (Table S2).

The effects of the numerical predictors remained consistent across different cover thresholds (i.e., ±0.5 % and ±10 %), with similar positive or negative influences on cover differences, though effect sizes varied (Fig. 5; Table S2). Positive predictors, the proportion of CoTS-preferred coral prey and years since disturbance, increased cover benefits more at higher cover thresholds, while coral larval supply, had a

consistent effect across all NLME models. The negative predictors coral habitat area and disturbance frequency increased cover deficits more at higher cover thresholds, while CoTS larval supply and years since control were consistent across all thresholds. Control frequency, a positive predictor, and CoTS density, a negative predictor, had greater effect sizes in the lower cover threshold models. Rubble maintained a consistent weak effect close to zero in all models.

While the spatial patterns for reef type were consistent across the ±0.5 % and ±5 % models, with priority and target reefs having more negative cover differences than the non-priority intercept, in the ±10 % model, target reefs had more positive cover differences compared to the non-priority intercept. Regionally, in the ±0.5 % model, far north, north and south reefs had more positive cover differences than the central intercept, while for the ±5 % and ±10 % models, all regions had more negative cover differences than the central intercept. All best models had positive intercepts (±0.5 % = 1.61; ±5 % = 5.91; ±10 % = 9.63) and moderate marginal and conditional R^2 values (marginal R^2 = 0.33–0.42; conditional R^2 = 0.35–0.43; Table S2).

4. Discussion

Since 2018, the Australian government's CoTS Control Program has coordinated a fleet of five to six vessels across the GBR, targeting approximately 200 reefs for control each year, then culling CoTS across those reefs to reduce their density to a point that coral growth can outpace CoTS damage (Fletcher et al., 2020; Matthews et al., 2024). While recent studies have demonstrated that the Control Program has successfully protected coral cover (Westcott et al., 2020; Matthews et al., 2024), we still have little understanding of which ecological and management factors are most important to maximising net coral growth.

Our results clearly demonstrate that CoTS control can generate substantial, and increasing, coral cover benefits at many reefs across the
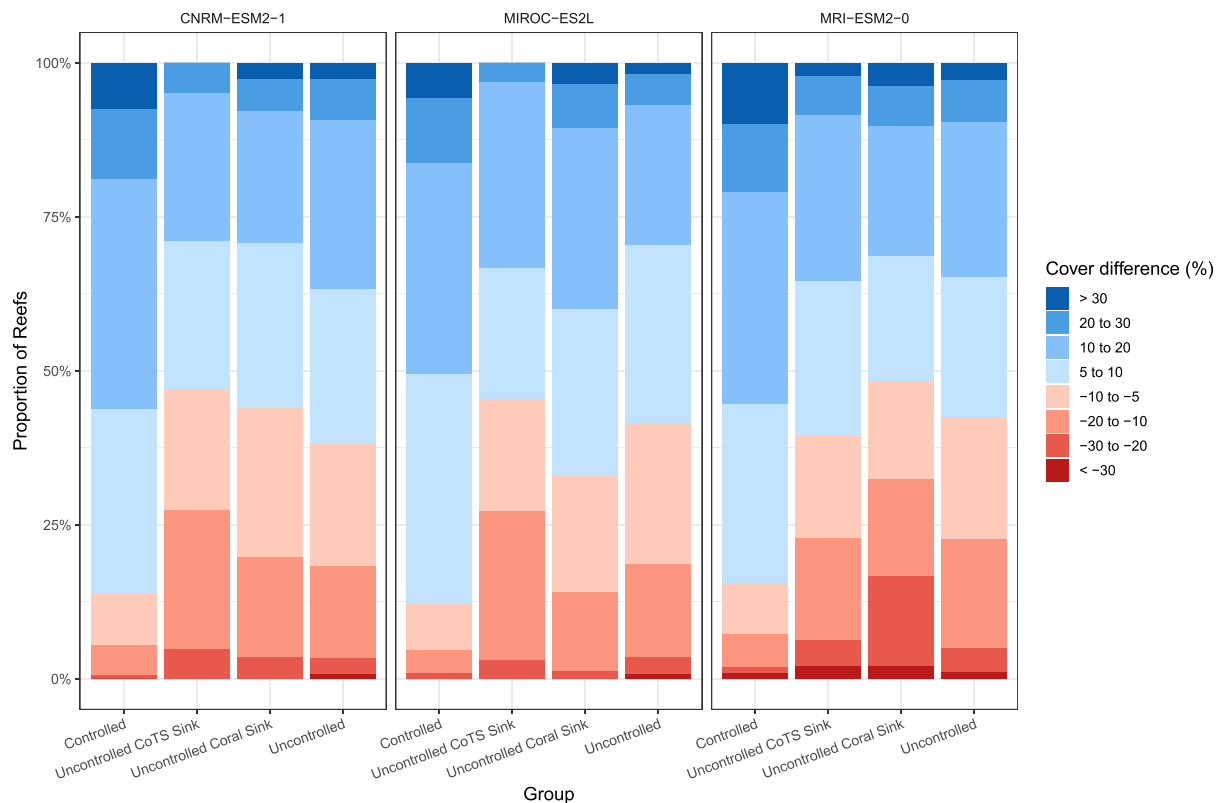
Fig. 3. Proportion of reefs within each cover difference (%; coral cover scenario – coral cover counterfactual) category (excluding −5 % to 5 %) across all simulation years (2019–2040) for each GCM scenario. Bars represent four reef groups: 1) controlled reefs where direct CoTS control was implemented, 2) uncontrolled reefs identified as CoTS sinks (>5 % larval input from controlled reefs), 3) uncontrolled reefs identified as coral sinks (>2.5 % larval input from controlled reefs), and 4) uncontrolled reefs that were neither controlled nor identified as sinks. Reef classification is dynamic: reefs are included as controlled from their first control event, as sinks from the first year they are linked to a controlled reef, and are excluded once they become impacted. Results are aggregated across all years.

GBR to 2040, even under divergent future climate trajectories. Importantly, our analysis, for the first time, identifies which factors contribute to the greatest coral cover benefits due to control, and identifies factors that contribute to the small number of cases where CoTS control generates a coral cover deficit. Our results show that a third of controlled reefs achieved cover benefits >10 %, with a fifth exceeding 20 %, while uncontrolled reefs, even those that were key sinks of CoTS or coral larvae, had reduced benefits and greater cover deficits. Benefits on controlled reefs accumulated over time, with gains becoming more pronounced later in the scenario. Reefs were more likely to experience benefits with increasing frequency of control, period between disturbances, and proportion of CoTS-preferred coral prey. High CoTS densities and CoTS larval supply and frequent disturbances reduced cover benefits, while rubble, coral larval supply, control recency, and coral habitat area had limited effects. Regional and reef-type differences emerged, with more pronounced benefits on reefs targeted for control and reefs in the north. Our results also demonstrated instances of negative cover differences. These were rarer (15.5 %), and generally small (<10 % coral cover deficit), and typically emerged immediately post-control. While our findings provide a lot of additional detail compared to previous studies, they broadly align with both previous modelling studies and empirical evidence (Westcott et al., 2020; Condie et al., 2021; Fletcher et al., 2021; Castro-Sanguino et al., 2023; Rogers et al., 2023; Matthews et al., 2024). Our GBR-wide simulations also provide insights that are difficult to obtain through fieldwork. Across reef types, our findings demonstrate sustained and increasing cover benefits from targeted, continuous CoTS control efforts over time and identify several key factors driving these outcomes.

The frequency of control interventions substantially positively impacted cover differences, with regular CoTS control events correlating

with increased cover benefits. These results align with numerous studies demonstrating that targeted, and importantly continuous, CoTS control is vital for maintaining coral cover and enhancing reef resilience due to the persistent nature of CoTS outbreaks (Westcott et al., 2020; Condie et al., 2021; Rogers and Plagányi, 2022; Castro-Sanguino et al., 2023; Matthews et al., 2024). Cover deficits began to disappear and cover benefits substantially increased after about 15 repeated control events, with the largest cover benefits mostly occurring within two years post-control. This highlights the importance of timely action in suppressing outbreaks and protecting coral cover (Babcock et al., 2020; Matthews et al., 2024). Beyond eight years post-control, both benefits and deficits tapered off, although there were also fewer model observations available. The absence of a longer control-free period could explain why the "Years Since Control" predictor had minimal influence in the models. While our results underscore the ecological benefits of frequent control, we acknowledge that such efforts come with significant logistical and financial costs. Identifying cost-effective strategies that balance the intensity and frequency of interventions with available resources remains a key challenge for (often resource-limited) managers and an important area for future research and planning.

Disturbance frequency consistently negatively affected coral cover, while the number of years since disturbance had a positive effect; more frequent disturbances reduced cover benefits, while longer disturbance-free periods increased them. In the model, cyclones and bleaching events cause immediate and severe coral mortality (Cheal et al., 2002; De'ath et al., 2012; Hughes et al., 2018). Although real-world disturbances can lead to longer-term ecological impacts, such as reduced coral survival after consecutive thermal stress (Hazraty-Kari et al., 2024) and macro-algal overgrowth on dead corals coupled with reduced herbivorous grazing and lower coral recruitment (Kopecky et al., 2024), these
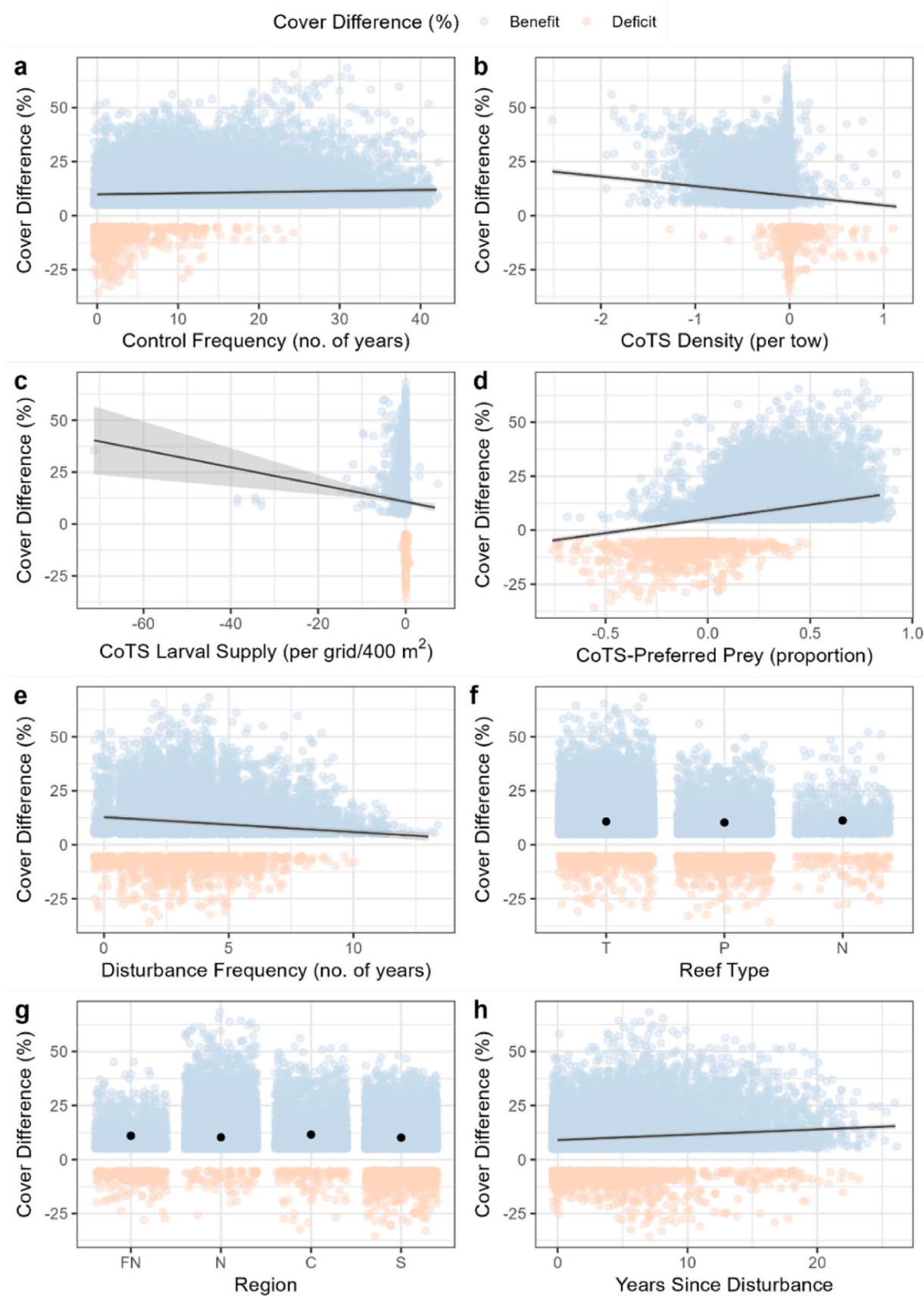
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Fig. 4. Cover differences (benefits: >5 % and deficits: < −5 %) on controlled reefs against the predictors from the best NLME model exploring the impacts of CoTS control between 2019 and 2040. **a**) Control Frequency: number of years control occurred prior; **b**) CoTS density (per tow): geometric mean change (delta) over the three years prior; **c**) CoTS Larval Supply (per grid/400 m2): geometric mean change (delta) over the three years prior (scaled); **d**) CoTS-Preferred Prey (proportion): mean change (delta) in the proportion of acroporids and pocilloporids over the three years prior; **e**) Disturbance Frequency: number of years disturbance occurred prior; **f**) Reef Type: Target (T), Priority (P), or Non-Priority (N); **g**) Region: Far North (FN), North (N), Central (C), or South (S); and **h**) Years Since Disturbance: number of years since the last disturbance. Points are individual model predictions (jittered) from all three climate models each with 20 individual runs, but reefs are only included from the first year that they are controlled. The black line is the regression from the best model with grey 95 % confidence intervals. Note that all predictors are on their original scales except for CoTS larval supply which has been centred and scaled to account for extremely high values.
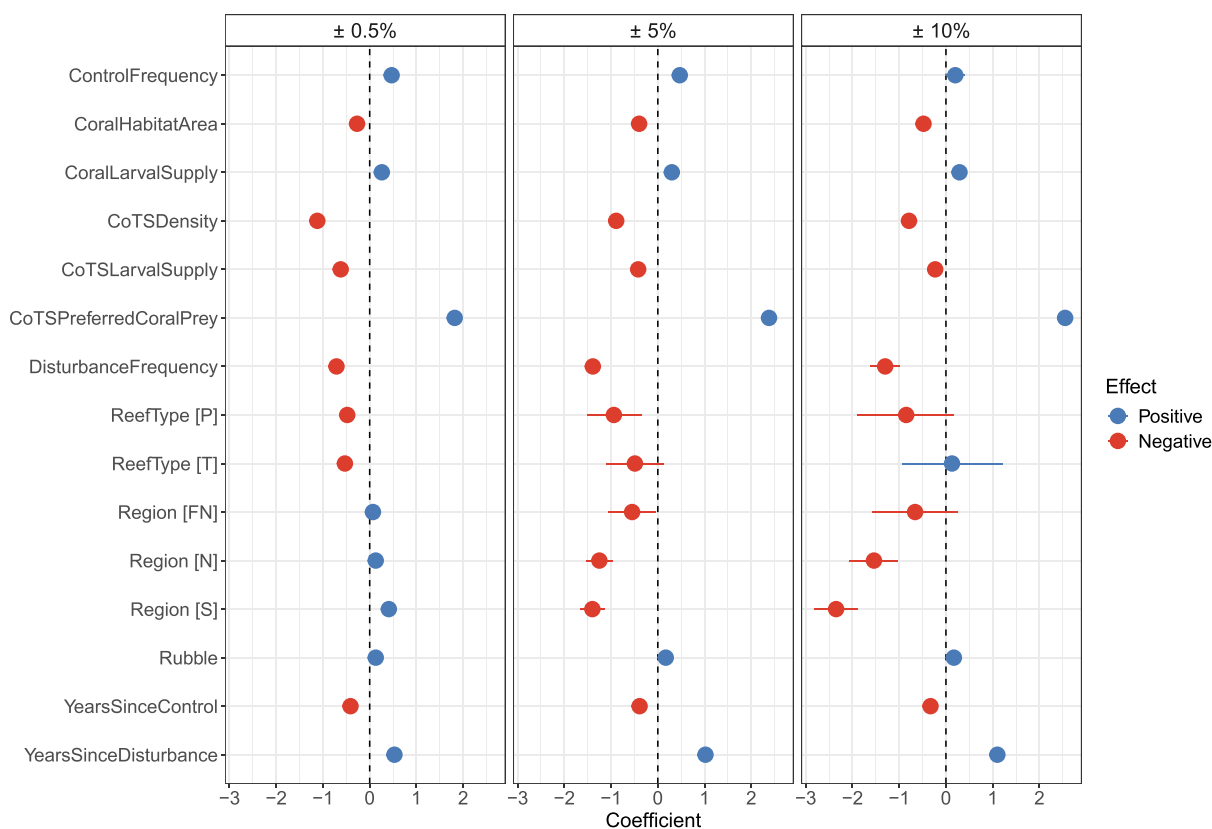

Fig. 5. Estimates and standard errors of cover differences (%) at three different thresholds (±0.5, 5, 10 %) for the predictors included in the best models exploring the impact of CoTS control on coral cover on controlled reefs. The predictors are standardised, so the coefficient of cover differences for that predictor represents a one standard deviation change in the corresponding predictor. The intercept represents the cover differences for non-priority (N) reefs located in the central (C) region.

processes are not directly modelled here. However, the model captures coral recovery potential and growth, which reflects similar outcomes following repeated disturbances. Notably, substantial cover benefits were still detected on some reefs even after frequent disturbances and immediately post-disturbance. Within the model, this suggests that effective CoTS control can help maintain coral cover or facilitate coral recovery after disturbance, mitigating their overall impact and enhancing resilience (Rogers and Plagányi, 2022). Coral cover on the GBR has shown substantial recovery potential despite increasing climate-driven disturbances (Emslie et al., 2024b), though ongoing global warming will likely exacerbate coral cover declines (Bohensky et al., 2011; Wolff et al., 2018; Mason et al., 2023). Moreover, our analysis focused on more severe disturbances (category cyclones ≥ 3 and Degree Heating Week ≥ 6), which may underestimate the cumulative effects of milder events on both coral cover and CoTS populations over time. Chronic disturbance regimes could become increasingly important in longer-term projections, especially as they may facilitate the build-up of macroalgae (not modelled here), which can suppress coral recruitment and slow recovery (Kuffner et al., 2006). The model does not yet incorporate chronic sub-lethal stress effects on coral, CoTS, or phase-shift dynamics, all of which may shape reef trajectories under

persistent low-intensity stress. Long-term projections would be strengthened by incorporating these processes as empirical data become available to inform their integration. Despite this, these findings support the need for regular CoTS management to maximise coral cover protection amidst disturbances (Babcock et al., 2014; Fletcher et al., 2020; Plagányi et al., 2020). Proactive and continuous management will be essential to safeguard coral reefs as disturbances intensify (Miller, 2015).

A higher proportion of CoTS-preferred prey corals, acroporids and pocilloporids, was one of the strongest positive drivers of cover benefits in our model. Within the model, increased availability of these corals reduces CoTS mortality from low coral cover. Culling CoTS on reefs with higher proportions of these coral groups will therefore generate larger benefits over the counterfactual scenario. Additionally, acroporids and pocilloporids are fast-growing species that facilitate rapid recovery after disturbances (Wakeford et al., 2008; Pratchett et al., 2020), a dynamic captured in the model. Our results indicate that reefs with a higher proportion of these genera experience more substantial recovery when protected from CoTS, while those facing recurrent outbreaks see slower recovery during disturbance-free periods due to reduced acroporid populations (Castro-Sanguino et al., 2021). However, both these genera

are also more vulnerable to bleaching events, both in the real world (Keesing et al., 2019), and in the model. Given their crucial role in reef ecosystem function and rapid recovery potential, targeted management strategies to protect these coral groups during periods of lower thermal stress are essential to maximise the long-term benefits of interventions (Ortiz et al., 2021).

As expected, higher CoTS densities reduced coral cover benefits and increased deficits across all NLME models. Adult CoTS are voracious coral predators (Keesing and Lucas, 1992; Pratchett et al., 2017); in the model coral consumption uses empirically derived individual size feeding rates and prey preferences (Bozec et al., 2022). Greater adult CoTS densities therefore cause greater coral losses and require increased control efforts. While CoTS larval supply had a strong negative effect on coral cover differences in the lower threshold NLME models, the effect was reduced in the ±10 % threshold model. In the real world, CoTS larvae disperse rapidly and extensively during outbreaks (Hock et al., 2014; Uthicke et al., 2015), showing exceptional resilience to varying conditions (Wolfe et al., 2017). Although aspects of these mechanisms are captured in the models, there is much that remains poorly understood regarding the transition from larvae and juveniles into coral-eating adults (Deaker et al., 2020; Pratchett et al., 2021; Wolfe and Byrne, 2024). Moreover, the model may need further refinement in representing fine-scale CoTS connectivity patterns (Skinner et al., 2024). Nevertheless, CoTS larval dispersal is known to play a critical role in outbreak dynamics in the real world (Kenchington, 1977; Moran et al., 1988), and is a key driver of cover deficits in our model.

Coral larval supply was a positive driver of cover benefits in our models. Although its effect was not as strong as other predictors, this confirms the importance of sustained larval supply in supporting coral recovery from CoTS management. In the model, coral larvae are critical for rapid reef recovery following disturbances (Richmond, 1997; West and Salm, 2003) and extensive coral loss (Bozec et al., 2022). In real world observations, coral larvae promote rapid increases in juvenile density and coral cover following severe cyclones (Lukoschek et al., 2013; Sato et al., 2018) and bleaching events (Gouezo et al., 2019), even on isolated reefs with limited connectivity (Gilmour et al., 2013). However, increasing disturbance frequency may compromise connectivity by reducing adult coral populations (Cheung et al., 2021) and impairing recruit survival on unconsolidated rubble beds (Chong-Seng et al., 2014; Kenyon et al., 2023). While both these processes are reflected in our model, broader ecological impacts likely extend beyond current parameterisations. Maintaining highly connected coral source reefs will be key to sustaining larval supply (McCook et al., 2009; Hock et al., 2017), and maximising the benefits of CoTS control. Indeed, while directly controlled reefs showed the greatest cover benefits, uncontrolled coral sink reefs had greater benefits than CoTS sink reefs in two of three climate scenarios. This highlights the critical role of coral larval supply in supporting recovery and suggests that, where resources are constrained, prioritising control on key coral source reefs may offer more effective outcomes than targeting CoTS sources. However, it should be noted that this analysis did not account for broader spillover effects on adjacent reefs beyond the first link in the network.

Rubble cover had a relatively minor influence in our models. Coral rubble typically indicates prior disturbance and reduced coral cover (Wolfe et al., 2021), but emerging evidence suggests it may play a more complex ecological role, potentially providing shelter for juvenile CoTS before they transition to coral predators (Deaker et al., 2020; Desbiens et al., 2023; Wolfe and Byrne, 2024). While our model accounts for the inhibitory effect of unconsolidated rubble on coral juvenile survival (by reducing survivorship in proportion to rubble area), it does not yet incorporate potential positive interactions between rubble and juvenile CoTS due to the current lack of robust empirical data. As rubble habitats are expected to increase due to climate change (Kenyon et al., 2023), integrating emerging field data on CoTS-rubble interactions (e.g., Wolfe et al., 2023; Wolfe et al., 2025) will be essential to improve model predictions and to better guide management responses in increasingly degraded reef environments.

Spatial patterns in coral cover differences reflected how reefs were prioritised for control by type and region. Target reefs showed higher absolute benefits due to earlier and more consistent interventions. However, these same reefs had negative coefficients in the two strictest (±0.5 % and ±5 %) cover threshold models, likely due to threshold sensitivity (positive effects increased in the ±10 % threshold model) and ecological complexity, where multiple interacting factors in the statistical model (beyond reef type alone) might obscure the effects of targeted control. Regionally, the far north showed the least absolute cover benefits. This is likely because fewer reefs were controlled there until much later in the scenarios, aligning with minimal historical culling (Matthews et al., 2024), despite emerging evidence of high CoTS densities (Vanhatalo et al., 2017; Pratchett et al., 2022). The north had the greatest cover benefits, followed by the central and southern regions. These patterns reflect known outbreak dynamics. In the north, the "initiation box" for CoTS outbreaks (Moore, 1990; Pratchett et al., 2014) contributes to higher background densities, which the model simulates by resetting populations to higher background levels, accounting for frequent outbreaks that disperse southward (Vanhatalo et al., 2017), and leading to large benefits from control. In the central, historically high CoTS densities, captured through manta tow survey data used to inform the model where available (Skinner et al., 2024), may have also offered more opportunities for control to rapidly improve coral cover (Vanhatalo et al., 2017; Matthews et al., 2024). In the southern Capricorn Bunker and Swain sectors, persistent outbreaks result from larval dispersal and hydrodynamic connectivity, both integrated into the model to reflect the flow of larvae from upstream regions (Miller et al., 2015). However, in the NLME models, the far north, north, and southern regions had reduced benefits relative to the central region in the ±0.5 % threshold model, but greater benefits in the ±5 % and ±10 % models. As with reef type, this likely reflects sensitivity to the cover thresholds and the complex ecological interactions leading to cover differences in the full NLME model. While these patterns offer useful insights, the model does not definitively identify the best areas for control. Instead, the results suggest that sustained management in regions showing benefits will likely support long-term coral resilience and recovery (McCook et al., 2009).

While these results deliver key insights into the drivers of near-term management benefits from CoTS control, several caveats must be considered. The scenarios analysed rely on one optimistic warming pathway (SSP1-2.6), but future warming may exceed 2 °C by 2100 (IPCC, 2023). Higher warming would accelerate coral declines (Mason et al., 2023), potentially reducing CoTS densities to the point where control is no longer necessary. However, this study focussed on outcomes to 2040, a period where climate futures do not majorly differ (Lee et al., 2021). Even within this window, variation across the three GCMs reflects differences in near-term warming trajectories, with MIROC-ES2L projecting the most severe coral declines. These model-specific differences underscore the value of using multiple climate models when evaluating management outcomes, even under a single emissions scenario. Yet, coral recovery following CoTS control may involve substantial time-lags, so short-term projections may underestimate longer-term benefits. The extent of these lags will depend on future CoTS densities and broader environmental changes. Assessments beyond 2040 should incorporate multiple SSPs, which differ markedly and carry greater climate uncertainty (Dubos et al., 2023; Bozec et al., 2025). Several important processes, such as coral adaptation (Lachs et al., 2024), ocean acidification (Kamya et al., 2016), warming impacts on CoTS biology (Pratchett et al., 2021), and changes in connectivity (Cheung et al., 2021), are not yet included in the model but may become more influential over longer timeframes. These factors, alongside the uncertainty regarding CoTS persistence under low coral cover, pose challenges for long-term management strategies. While crucial for future long-term scenario assessments, they lie beyond the scope of current recommendations, which are focused on near-term, actionable

outcomes. It is also important to note that we used a fixed ecological threshold (0.04 CoTS/min) to reflect the current control program, which is effective for preventing coral loss. However, a more targeted approach aimed at improving coral cover may require an adaptive threshold based on the most prevalent corals in the local community (Rogers et al., 2024). Some biological parameters were also simplified due to limited empirical data, particularly for juvenile stage duration and predation (Pratchett et al., 2021) and outbreak triggers (Pratchett et al., 2014). Even small uncertainties in these parameters can influence long-term dynamics, so results should be interpreted as indicative of trends rather than precise forecasts. However, prior validation of our CoTS predictions against in situ manta tow survey observations showed high congruence: ~81 % of categorical reef level CoTS densities matched or differed by only one category (Skinner et al., 2024), supporting the model's use as a tool for assessing the benefits of CoTS control.

Our results also demonstrated instances of negative cover differences. These were rarer (15.5 % of differences) than benefits (85.5 % of differences), and generally small (<10 % coral cover deficit), and typically emerged immediately post-control. These deficits, while counter-intuitive, likely result from several mechanisms. First, the stochastic implementation of ecological processes in the model introduces variability, as once control is initiated, CoTS populations and hence coral cover become non-identical between the control and counterfactual scenarios, even under identical external conditions. Second, in the model, CoTS populations are controlled to an ecological threshold which is larger than the "background" density of CoTS populations that experience natural collapse. This may lead to slightly greater coral losses at some controlled reefs in the control scenario, if that same reef experienced a CoTS population collapse in the counterfactual. Once the CoTS populations are controlled, the recovery trajectory could differ: in the counterfactual, coral cover might drop but rebound more quickly once CoTS collapse naturally, while under control, recovery is slower but steady due to the maintained low CoTS density. This dynamic could help explain the initial cover deficits in controlled reefs despite the long-term benefits of CoTS control. A real world version of this hypothesis has been discussed in the literature (Moran, 1986; Zann et al., 1987, 1990), but further study would be required to understand its operation in the model. Our results show that, whatever the mechanism, the effect is small relative to the benefit generated by CoTS control.

Our findings confirm that controlling CoTS populations on the GBR enhances coral cover and supports ecosystem function, even as climate-driven disturbances intensify (Condie et al., 2021; Rogers and Plagányi, 2022; Castro-Sanguino et al., 2023; Matthews et al., 2024). The greatest benefits were on reefs with frequent targeted control, infrequent disturbances, and high proportions of CoTS- preferred coral prey. Cover benefits decreased with higher CoTS densities and CoTS larval supply, and varied by reef type and region, reflecting differences in control efficacy and the distribution of controlled reefs. While our study identifies factors that both enhance and limit the effectiveness of current control efforts, our results clearly show that CoTS control delivers significant, and increasing, coral cover benefits at many reefs across the GBR through to 2040, even under current and projected climate conditions. Proactive and multi-faceted management strategies will be critical for protecting coral cover and the ecosystem health of an increasingly disturbed GBR.

CRediT authorship contribution statement

Christina Skinner: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Yves-Marie Bozec:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Cameron S. Fletcher:** Writing – review & editing, Supervision, Methodology. **Peter J. Mumby:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Peter Mumby reports financial support was provided by Australian Government Department of Climate Change, Energy, the Environment, and Water. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.126627.

Data availability

Data will be made available on request.

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