nature portfolio

Peer Review File

Local anthropogenic stressors outpace climate impacts on coral reef collapse in the northern South China Sea

Corresponding Author: Professor Hongwei Zhao

This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)
This manuscript addresses an important and often overlooked aspect of reef conservation – providing a holistic view of all potential stressors, and balancing the consideration of local over global stressors, using the South China Sea as a case study. The study results with well argued recommendations for integrated coastal reef management strategies. The supporting data are thoroughly compiled and comprehensive (although many of them don't seem to be used in the analyses?)
The study is based on two sets of analyses – panel regressions and structural equation models.

It is unclear what classifies as 'global' stressor. Heat stress is not incorporated into pane; regression nor SEM. Other consequences of climate change are difficult to factor in (more intense floods, more intense typhoons, ocean acidification). So the conclusion, while plausible, has to be taken with some precaution.

The panel regression analysis needs some further clarification. Why does the analysis shown in Fig 2a only include some variables, eg not degree heating weeks? Wouldn't it be informative to separate destructive fishing (with their direct impact on coral) from the 'overfishing' impact (causing more indirect impacts on reef food webs)? What about nutrients, what about coastal development? At present, it remains unclear whether fish density is a driver of coral cover, or a response to coral cover, although the discussion suggests it is the main driver of coral cover. Dito for macroalgae (reduced coral cover may provide more space for algae). Hence causal relationships remain unresolved, one of the problems of regression analyses (they really show associations not causation).

I didn't understand why some of the putative drivers (COTS, fish densities) are plotted as time series in Fig 1 while some other drivers are plotted in Fig 2 b-e (time series on pressures), and others were not shown at all (nutrients, agriculture).

Some results appear surprising. Eg macroalgae appear to be a strong 'driver' for HNXS, although macroalgae are very low throughout that region (Fig. 1d). In contrast, the analyses suggest no typhoon impact on coral cover, despite high typhoon exposure in 2009-2014. Also, turbidity is high and variable at HNE where it is suggested to have a positive effect on coral cover, whereas turbidity is lower and even in HNS but with a negative effect on coral cover (both contrary to known biological knowledge)?

The patterns in the remote Xisha Islands, without resident population, without agricultural runoff, and fish densities that are still higher than in the other two regions, are not supportive of the idea of local impacts, and some of the patterns remain unresolved. (Except, does Line 125: does the reference to 'side-in (perturbations causing direct coral mortality and habitat loss)' include the massive naval base constructions that have recently been reported from some of the Xisha Islands?) If yes, such massive development activities should be included as a separate driver in the analyses to test for their impacts. If no, what evidence is there for local impacts on these remote islands? Fig 1 suggests that COTs seem the main driver of coral loss in HNXS, but it is questionable whether COTs should be classified as 'local' driver.

The SEM should be an easy-to-follow, effective tool to analyse the complex data and visualise the results; however many of their results appear contrary to known biological knowledge and inconsistent across regions, suggesting problems with the model structure or the analyses. For example, the positive links between SST and both macroalgae and COTs in HNXS is not based on known ecological knowledge, and the apparently strong COTS effects are not emerging from the SEM shown in Fig 3. For HNE: resident population was found with a negative effect on macroalgae, what is the biological basis for this (in HNS it is positive)? In HNS, agriculture doesn't affect turbidity or macroalgae, but in HNXS, fish densities increase turbidity? Etc.It is difficult to tell what is going on, but a separation of destructive fishing and fish densities may help here.

Finally the model results (in Fig 5) suggest the improvement of coral cover given region specific tailored management action based on land-based interventions, such as nutrient reduction, fishing quotas, and CoTS control. Would it be more informative to show a matrix of all three main management actions at disposition for all three regions? At present, the case study 1 mixes up nutrients and COTs removal, why?

Reviewer #2

(Remarks to the Author)
Summary
This paper leverages a long-term data set (1990s to 2020) for the northern South China Sea to identify key drivers for coral cover decline in the region. Through regressions and structural equation modeling, the authors find that local anthropogenic stressors are collectively stronger predictors for live coral cover than climate associated drivers. Additionally, the authors perform simulations to test the effects of hypothetical mitigation scenarios on live coral cover in the region.

Major comments
I think this paper has potential. The major finding of this paper—that local stressors are collectively more important than global stressors—is important and timely. There is a growing body of literature showing that local stressors can have significant effects, but from my understanding that literature does not necessarily claim that local stressors are more important. This paper highlights the importance of mitigating local stressors for coral conservation. I also appreciate that this study is focused on a region that is relatively understudied for coral reefs systems. With careful attention to improving readability and clarifying key concepts, this study could be a key contribution to the literature connecting various stressors to coral cover.

Minor comments
With that being said, I found this paper quite hard to follow for a couple of primary reasons that the authors should carefully address. First, there is an excessive use of acronyms. I think the authors should try to use acronyms as sparingly as possible. For example, I don't think it necessary to shorten 'live coral cover,' 'South China Sea,' 'Integrated Coast-Reef Management,' etc. I know that the sites (HNE, HNS) sometimes refer to several regions, but I think renaming those to something like 'Hainan East' and 'Hainan South' would greatly improve readability. Second, there were some incomplete or vague sentences throughout that need to be fixed. Several conclusions also appear to overstate what can be reasonably inferred from the results. I will do my best to point these out in the Line Edits section.

In terms of key concepts that need clarification, the authors need to fully explain how tourism was quantified. Lastly, I read through the Supporting Information and the approach for evaluating the hypothetical scenarios was not explained. Was the structural equation model used?

Line edits
General note: Fix the term "agriculture N" to "agricultural N" throughout the manuscript
70: Suggest removing 'being'
79: Change 'industry' to 'industries'
80: missing part of sentence after 'areas'; inappropriate expansion of what?
88: Further improvement in terms of or relative to what exactly? Do you mean that new approaches have been developed?
92: If this is what you mean, I suggest rephrasing to "Focusing on the northern South China Sea, an urbanized reef hotspot, …"
96: What does telecoupled mean?
106: Missing part of the sentence?
107: "in an anthropogenically"
118: This is an example of excessive acronyms that make the paper very difficult to follow for an unfamiliar reader.
122: Change to coral reefs
148-150: These references seem to be regionally constrained to South China Sea, so I suggest modifying this sentence to reflect that.
177: This is a potential/plausible mechanism that I don't think is directly supported by this study. I suggest adding "fishing COULD initiate a critical …"
163-183: This entire last section should be written so that it's clear that these are your hypotheses/interpretations of your findings.
201: Change 'agriculture nutrients inputs overload' to 'agricultural nutrient inputs' or similar
203: Remove 'in HNE'
206: Remove 'a part of'
208: change 'agriculture' to 'agricultural'
219: change 'enhances' to 'enhancing'
225: Hysteresis is a specific mathematical pattern that your study does not directly show. Suggest stating "potentially leading to hysteresis in reef …"
230: Incomplete sentence
252: Remove 'with'

255: Make sure to explain how you are dealing with tourism
272: Change ‘outbreak’ to ‘outbreaks’
279: Change ‘predators’ to ‘predator’
286: ‘in the food chain’
290: Change ‘reefs’ to ‘reef’
298: Incomplete sentence
309: Not sure if MC is defined but I think these factors should all be spelled out
310: Incomplete sentence
322: Change ‘considering’ to ‘under’
347: “could be more helpful”?
356: Change ‘has’ to ‘have’
373-386: To me, this reads more like a Conclusions/Summary section rather than Conservation Implications. Suggest changing the subheading or re-writing or re-organizing this paragraph to be more about Conservation Implications.
407: Change ‘transplant’ to ‘transplantation’
415: What do you mean by sieving?
418: What is (remove)?
418: What do you mean by reef check survey and by simple random sample survey? please elaborate
432-443: This paragraph is written in present tense while the previous paragraphs were written in past tense.
440: Change ‘dynamics’ to ‘dynamic’ and ‘agriculture’ to ‘agricultural’
464: “through an ordinary least squares”
475: “Beta_k is the estimated coefficient” and “gamma is the spatial autoregressive coefficient”
479: construct piecewise structural… OR conduct piecewise structural equation modeling
491: Incomplete sentence (starting “our initial model”)
492: Change “result” to “results”
502: What does keep more than 10% mean?

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)
I have read the manuscript again and the rebuttal letter. The Authors have carefully and thoughtfully addressed my earlier concerns both in the letter and in the revised manuscript. I find the manuscript is now much easier to follow, the choice of data, figures, methods and findings are clearly explained, and the conclusions well supported, with some important adequate caveats added. This quantitative empirical study will become a very important and both internationally and nationally useful contribution to the scientific literature on the topic.

Reviewer #2

(Remarks to the Author)
I'm satisfied with how the authors addressed feedback from myself and the other reviewer. I appreciate the thorough responses and the added text/edits have greatly improved the clarity. The added text could use some careful proofreading(e.g. L81 nutrient -> nutrients, L536) but otherwise I have no further feedback.

Nature Communications

Peer Review File

Manuscript Title: Local over Global: Anthropogenic Stressors Outpace Climate Impacts on Coral Reef Collapse in the South China Sea

Manuscript ID: NCOMMS-25-31595A

Response to Reviewers' Comments

We thank the two reviewers for their positive evaluations and valuable feedback. Below, we address each reviewer's comment in sequence. Reviewers' comments are in black, and our responses are highlighted in **blue.** Revisions made to the manuscript are included in **red in the manuscript document.**

Reviewer #1 (Remarks to the Author):

This manuscript addresses an important and often overlooked aspect of reef conservation – providing a holistic view of all potential stressors, and balancing the consideration of local over global stressors, using the South China Sea as a case study. The study results with well argued recommendations for integrated coastal reef management strategies. The supporting data are thoroughly compiled and comprehensive (although many of them don't seem to be used in the analyses?). The study is based on two sets of analyses – panel regressions and structural equation models.

Response: We thank the reviewer for the valuable feedback and for recognizing the importance of our holistic approach. The comprehensive dataset was essential for our analysis. The exclusion of some variables from the final statistical models was a deliberate step to ensure statistical robustness, following a rigorous screening process to avoid multicollinearity and ensure data suitability. Variables with a correlation coefficient $|r| > 0.7$ or a Variance Inflation Factor (VIF) > 5 were removed. Furthermore, only variables with at least five consecutive years of monitoring data were included in the formal driver analyses (panel regressions and SEM) to maintain temporal consistency. While some discrete or highly collinear variables (e.g., mangrove/seagrass area, some water quality parameters) were not included in the final models, they were vital for preliminary analyses and for providing a complete ecological context in the discussion. This approach balanced statistical rigor with a comprehensive ecological perspective.

Please find below our point-by-point response to your comments.

It is unclear what classifies as 'global' stressor. Heat stress is not incorporated into panel regression nor SEM. Other consequences of climate change are difficult to factor in (more intense floods, more intense typhoons, ocean acidification). So the conclusion, while plausible, has to be taken with some precaution.

Response: We thank the reviewer for raising this critical point. We fully agree that distinguishing between "local" and "global" stressors can be complex. In our study, we define global stressors as basin-scale processes largely independent of local management, such as typhoon exposure, ocean warming (heat stress) and acidification. All of these variables were incorporated into the initial variable pools for both panel regressions and SEM. After standard collinearity screening ($|r| < 0.7$ or VIF < 5 and convergence checks, SST_{warm} remained in the final models, which measures mean SST in warm months from May to October indicating heat stress and typhoon exposure (typhoon damage coefficients, TDC). DHW_{max} was removed because it covaried strongly with SST_{warm} ($r = 0.68 \sim 0.81$, Fig. S2a) and DHW_{max} are indirectly included as SST_{warm}, while extreme rainfall covaried with typhoon exposure. And the extreme flood events are closely related to typhoon activity in our study region, allowing the TDC to also serve as a proxy for flood-related impacts. Surface pH showed insufficient within-region temporal variability to improve model fit. Thus, the reported coefficients quantify the portion of coral-cover change attributable to the retained local and global drivers given the available 2002–2014 data. It is worth noting that this study timeline is the background of dynamic change and ongoing global warming. We have added this clarification to Methods **(lines 464, 474-479)** and now state the limitation explicitly in Supplementary Methods **(lines 97, 120–125, 205-215).**

We agree with the reviewer that our conclusions should be interpreted with this limitation (Spatio-temporal framework). We have now revised the discussion section to explicitly state that our findings on the dominance of local stressors are valid within the scope of our analytical framework **(see lines 135, 168-169)**. We have also added a sentence to our conclusion to recommend future studies that integrate broader and fine-scale data **(see lines 408)**.

See lines 464: "These covariates are included: coral species (CS), reef fish density (Fish, indicates the status of fishery resources on coral reefs and can inversely represent the intensity of fishing), macroalgae coverage, typhoon exposure, **temperature (SST_{warm}, mean SST in warm months (May to October each year))**, turbidity (K_d490), local human resident population (POP, denotes the potential interactions and accessibility between local human settlements development and coral communities [e.g., water quality and land use], also known as human gravity); and agricultural development (agricultural N, denotes total agricultural nitrogen emissions per year to the local waters)."

See lines 474-479: All environmental variables underwent preliminary testing analysis, including Pearson correlation analysis, Principal Component Analysis (PCA), and a Variance Inflation Factor (VIF) check. To avoid multicollinearity, we rigorously removed variables with a correlation coefficient $|r| > 0.7$ and VIF > 5. And variables were prioritized if they had a greater contribution to the primary axis components in PCA. This step is crucial to avoid statistical artifacts and to ensure that the independent effects of the included variables could be accurately and reliably estimated.

Supplementary Methods

See lines 97: For each site, we calculated the mean SST in the year and mean SST from May to October each year (in warm months, SST_{warm}).

See lines 120–125: Global stressors were pre-defined as basin-scale processes largely independent of local management. In this study, typhoon exposure could be considered as a global stressor which is largely independent of local management. And every storm covers the entire subregion with uniform destructive power, so its impact—like that of heat stress and other climate variables—cannot be distinguished among study sites within any single time frame.

See lines 205-215: Variable selection. The exclusion of certain variables from our final statistical models was a result of a rigorous data screening process to address collinearity and temporal coverage scale **(≥5 years)** to ensure statistical robustness. While some water quality and local environmental variables were not included in the final models due to these collinearity issues **(Fig. S2 & Table S2)**. For example, Degree-heating-weeks (DHW_{max}) covaried strongly with SST_{warm} (r =0.68 ~ 0.81), and Principal Component Analysis (PCA) confirmed that SST_{warm} had a greater primary axis component than DHW_{max}, indicating SST_{warm} was the more representative variable for heat stress in our dataset. Therefore, DHW_{max} was excluded to avoid multicollinearity and ensure the robustness of our models. To balance statistical rigor with a holistic ecological perspective, the excluded data were not discarded but were instrumental in our preliminary analyses and in strengthening the overall narrative of our findings.

See lines 135: Consistently, both show that human activities, including fishing pressure and economic development, are the major determinants of LCC **in this study**.

See lines 168-169: Given this urgency, isolating and mitigating the impacts of controllable local stressors can provide crucial buffer time for the survival of coral reefs.

See lines 408: Future studies that integrate broader scale and fine scale data are recommend.

The panel regression analysis needs some further clarification. Why does the analysis shown in Fig 2a only include some variables, e.g. not degree heating weeks? Wouldn't it be informative to separate destructive fishing (with their direct impact on coral) from the 'overfishing' impact (causing more indirect impacts on reef food webs)? What about nutrients, what about coastal development? At present, it remains unclear whether fish density is a driver of coral cover, or a response to coral cover, although the discussion suggests it is the main driver of coral cover. Dito for macroalgae (reduced coral cover may provide more space for algae). Hence causal relationships remain unresolved, one of the problems of regression analyses (they really show associations not causation).

Response: We deeply appreciate the reviewer's comments and the request for further clarification on our variable selection and panel-regression design.

Variable selection.

All candidate environmental variables were included in an initial pool for preliminary analysis, including correlation analysis, Principal Component Analysis (PCA), and a Variance Inflation Factor (VIF) check. We retained only those that met two criteria: (i) $|r| < 0.7$ and VIF < 5 after collinearity screening, (ii) temporal coverage scale ($\geqslant$ 5years). As Degree-heating-weeks (DHW_{max}) covaried strongly with SST_{warm} ($r = 0.68 \sim 0.81$, Fig. S2a), and Principal Component Analysis (PCA) confirmed that SST_{warm} than DHW_{max} had a greater primary axis component **(Fig. S2c)**, indicating SST_{warm} was the more representative variable for heat stress in our dataset. Therefore, DHW_{max} was excluded to avoid multicollinearity and ensure the robustness of our models. We have added this clarification to Methods (**lines 474-479**) and Supplementary Methods (**lines 97**, **120 – 125)**.

We appreciate the reviewer's suggestion regarding the differentiation of fishing impacts, an approach we also considered in our initial analysis. However, it is difficult to separately record destructive fishing (blast and cyanide) and overfishing (fishing nets and traps) in the field surveys. While distinguishing between destructive fishing and indirect overfishing impacts is worth exploring, precise and long-term quantification to separate these dynamic activities remained challenging. To address this challenge, we compiled a comprehensive dataset of four fishing indicators, including data from the Global Fishing Watch (GFW), the number of fishing vessels, fishing production, and fish density **(Fig. S8 & Fig. 1e)**. After rigorous data screening, only fish density was found to meet the necessary statistical criteria for inclusion in our final models. Both forms of fishery activities were loaded on the same latent variable-fish density in this study **(Fig. 1e)** and cannot be disentangled statistically without over-parameterising the data of temporal and spatial accuracy. The other three indicators **(Fig. S8)** were also retained as supporting data to corroborate our findings, thus enhancing the overall credibility of our results.

The panel-regression analysis focused on the exploration of the impact of proximal ecological factors on the live coral coverage. Here, macroalgae and turbidity were the more representative proximal variable for nutrients (DIN) and coastal development based on the screening criterion.

Causal inference.

The observational data cannot prove causation without a careful research design that includes exogenous shocks. Panel regression alone is insufficient to establish causal inference. Endogeneity is addressed in two ways. First, we used lagged predictors (t-1) in all panel regressions, so fish density and macroalgae coverage precede the coral-cover response by one year (Brüderl et al., 2015). Second, SEM explicitly models directional paths based on a priori ecological knowledge (Fig. S3 & Fig. 3a), the fit is rejected if causal arrows are reversed. These safeguards make the proposed directionality the most parsimonious explanation. We have clarified these details in Supplementary Methods **(lines 215-219 and Fig. S3)**.

Supplementary Methods

See lines 215-219: Panel regression alone is insufficient to establish causal inference. Endogeneity is addressed in two ways. First, we used lagged predictors (t-1) in all panel regressions, so fish density and macroalgae coverage precede the coral-cover response by one year. Second, SEM explicitly models directional paths based on a priori ecological knowledge (Fig. S3 & Fig. 3a); These safeguards make the proposed directionality the most parsimonious explanation.

Fig. S3. Conceptual models showing linkages and feedbacks between anthropogenic activities and coral communities and the initial model for structural equation model (SEM) exploring the effects of environment variables on live coral coverage. a) Conceptual models showing linkages and feedbacks between anthropogenic activities and coral communities in coastal subregions **(in manuscript, ref. 2, 38, 49, 51, 62-64, 71, 73-74, 80)**. Drivers are traits in social-economical systems that indirectly influence how people interact with coral reefs. Stressors directly affect coral reef ecosystems. Single-headed arrows indicate how the pathway flows from drivers to stressors and coral reef. Double-headed arrows show the complex linkages and feedback that also occur between the various components. Modified from Hughes et al. (2017).

I didn't understand why some of the putative drivers (COTS, fish densities) are plotted as time series in Fig 1 while some other drivers are plotted in Fig 2 b-e (time series on pressures), and others were not shown at all (nutrients, agriculture).

Response: Thank you for pointing out the differences in the figures. The figure organization is not arbitrary; rather, it follows the logical progression of our analysis, moving from establishing the baseline status of the coral community to exploring the hierarchical influence of its drivers (Hughes et al., 2017).

Fig. 1 serves to establish the initial state and spatial heterogeneity of the coral reef community. By presenting key biological indicators like live coral cover, macroalgae, CoTS density and fish densities, it visually sets the stage for the subsequent analyses by showing the trends and spatial variability of our response variables.

Fig. 2 moves from community status to analyzing its direct or proximal drivers. This is where our panel regression analyses quantify the effects of key environmental and biological stressors. The time series plots in Figures 2b-e are included here to visually demonstrate that the key environmental factor variations are closely related to the temporal dynamics of the decline in live coral coverage. Plotting them alongside the model coefficients (Fig. 2a) makes it clear that the timing and strength of each disturbance episode shape its impact on coral cover.

Fig. 3 follows the same principle for the socio-economic drivers the back of the causal chain, so the time series plots of agricultural nitrogen and POP are shown together with SEM analysis. Figure 3b-c exhibited marked regional differences in both magnitude and temporal pattern. Plotting them alongside the model coefficients

(Fig. 3a) makes it clear that the timing and strength of each disturbance episode shape its impact on coral cover. In SEM analysis, agricultural nitrogen and POP were the more representative distal variable for nutrients and coastal development.

Some results appear surprising. Eg macroalgae appear to be a strong 'driver' for HNXS, although macroalgae are very low throughout that region (Fig. 1d). In contrast, the analyses suggest no typhoon impact on coral cover, despite high typhoon exposure in 2009-2014. Also, turbidity is high and variable at HNE where it is suggested to have a positive effect on coral cover, whereas turbidity is lower and even in HNS but with a negative effect on coral cover (both contrary to known biological knowledge)?

Response: We appreciate the reviewer's careful scrutiny of our results, which highlights the complexity of multi-driver systems. We agree that some findings for macroalgae, typhoons, and turbidity seem appear surprising at first sight, but these results are ecologically reasonable when considering unique baselines, temporal dynamics and interactions of multi-stressors at each subregion.

Macroalgae and typhoon exposure in HNXS.

The effect of a driver is dependent on its timing relative to the coral community's state. While macroalgae coverage was low overall **(Fig. 1d)**, it showed a localized and temporary increase during 2009 to 2012, immediately following the mass mortality event (2005-2009). Our panel model captures that macroalgae has a weak but significant negative effect on a depleted system, as it likely hindered the survival and recovery of the surviving corals. As shown in **Fig.1a**, live coral coverage of HNXS dropped sharply from 2005 to 2009, reaching its lowest level in 2011. This continuous declines in live coral coverage coincided with short-lived bloom in macroalgae. Thus, the panel model attributes part timeline of that decline to the transient macroalgal pulse, even though long-term mean coverage is low.

However, the high typhoon exposure occurred later, during 2012 to 2013. At this point, typhoons likely affected the recovery process but did not cause a substantial and additional reduction in live coral, thus imposing no significant effect on the overall live coral cover trend captured by our models. This temporal relationship of disturbance and coral community's state explains why our model showed an impact from macroalgae but not from typhoons.

Turbidity in HNE and HNS.

The seemingly contradictory results for turbidity in HNE and HNS are also a function of local context and multi-causal interactions. In HNE, the baseline turbidity is relatively high, and the dominant coral species are more stress-tolerant. In a warming ocean, high turbidity can provide a protective effect by shading corals from excessive light and thermal stress, which has been documented in other studies (Sully et al., 2020; Zweifler et al., 2021; Xing et al., 2012). For instance, Sully et al.(2020) found that K_d490, a measurement positively related to turbidity, between 0.080 and 0.127 reduced coral bleaching during thermal-stress events. The final model result represents the net effect of this turbidity, which, in conjunction with other variables (e.g. temperature), appears to mitigate overall coral loss. At HNS, while the overall turbidity is lower, the negative effect coincides with a period of significant spikes in turbidity from 2007–2010. These spikes, likely caused by impacts from coastal development, led to high sedimentation rates and the loss of sensitive coral species, which is supported by our data and other studies (Li et al. 2013). Additionally, if the storm occurs in the same year as the macroalgae pulse and the turbidity peak, their respective contributions are segmented among these relevant predictors. In short, these anomalies result from non-linear, time-specific interactions rather than model artefacts.

We now clarify this with more explanation in the revised manuscript **(lines 213-211)** and Supplementary Information. These results highlight a key finding of our study, that the impact of any given stressor is highly dependent on the local ecology baseline (e.g. species composition and environmental background), the disturbance's timing and intensity, and interactions with other stressors.

See lines 203-211: Our findings demonstrate that LCC trajectory is governed by interacting socioeconomic factors beyond fisheries, with agriculture expansion, urbanization and tourism collectively exacerbating land-based nutrient loading, bioerosion and coastal habitat modification. Nearshore reefs in Hainan East and Hainan South have experienced disproportionately higher anthropogenic pressures compared to remote reefs in Hainan Xisha, reflecting differential exposure to stressors derived from regional socio-economic development. Our results highlight the key finding that the impact of any given stressor is highly dependent on the local ecology baseline (e.g. species composition and environmental background), the disturbance's timing and intensity, and interactions with other stressors.

The patterns in the remote Xisha Islands, without resident population, without agricultural runoff, and fish densities that are still higher than in the other two regions, are not supportive of the idea of local impacts, and some of the patterns remain unresolved. (Except, does Line 125: does the reference to 'side-in (perturbations causing direct coral mortality and habitat loss)' include the massive naval base constructions that have recently been reported from some of the Xisha Islands?) If yes, such massive development activities should be included as a separate driver in the analyses to test for their impacts. If no, what evidence is there for local impacts on these remote islands? Fig 1 suggests that CoTS seem the main driver of coral loss in HNXS, but it is questionable whether CoTS should be classified as 'local' driver.

Response: We thank the reviewer for these important questions, which address a key ecological nuance of our study. We agree that the patterns at HNXS, the remote reefs, require careful clarification. Although the pattern is not driven by typical land-based stressors, there are still other local stressors, such as fishing pressure or predation by natural enemies.

Evidence of local impacts.

Although the HNXS have no permanent residents or agriculture, they have been subject to persistent, local-scale fishing by distant-water fleets. The HNXS case is, in fact, a prime example of a local impact driven by long-term fishing disturbance, rather than by agricultural runoff. Furthermore, our analysis is based on within-region comparisons over time, not cross-regional comparisons. While fish densities at HNXS remain higher than those in the other two regions, our data show a 60% decline in fish density relative to its baseline in 2002, a significant reduction that our model captures as a key local stressor for LCC decline. This substantial decline and long-term low level in fish abundance **(Fig. 1 & Fig. S9b)** are a direct result of localized overfishing from distant-water fleets and represents a critical local stressor.

The "side-in" perturbations and coastal constructions (e.g. naval-base constructions).

We have proposed three non-exclusive scenarios: the top-down (overfishing), bottom-up (eutrophication and pollution) and side-in (perturbations causing direct coral mortality and habitat loss) models (Pratchett et al., 2017; Precht et al., 2019). The "side-in" refers to acute events that cause direct coral mortality, such as fishing and CoTS outbreaks in this study, and it does not include large-scale coastal constructions (e.g. naval-base constructions). This can be supported by the turbidity (**Fig.2c,** remote sensing monitoring) suspended solids variation (**Fig.S10i**, cruise monitoring), which represents major coastal construction impacts. There is no significant increase in turbidity during the period of substantial LCC decline from 2005 to 2009, and our models did not capture turbidity as a key local stressor in HNXS. The evidence for local impacts on HNXS is a tightly coupled timeline where a sharp decline in fish density and CoTS outbreaks coincided with an abrupt crash in live coral coverage. We have expanded these points in the revised Supplementary Methods **(lines 140)** and Discussion **(lines 294)** to clarify how local drivers operate in HNXS.

Whether CoTS should be classified as 'local' driver.

While a CoTS outbreak can look like a natural event, it can be classified as a local driver of reef degradation. This is because CoTS outbreaks, though not caused by humans directly, are often triggered or exacerbated by human-induced local stressors (Pratchett et al., 2017; Skinner et al., 2025). The detailed explanation is as follows: **(1) The Causal Link to Local Stressors.** The most compelling argument for classifying CoTS outbreaks as a local driver is their ecological link to overfishing. Many of the fish and invertebrates that prey on CoTS (both as larvae and as adults) are the same species targeted by fisheries (Pratchett et al., 2017). When these predator populations are severely reduced by fishing pressure, the natural control on CoTS populations is removed. This imbalance can lead to a surge in CoTS numbers, culminating in a destructive outbreak that decimates coral reefs. Since overfishing is a local and manageable stressor, the resulting CoTS outbreak can also be seen as a localized, indirect consequence of human activity. **(2) A Site-Specific Phenomenon.** CoTS outbreaks are a highly localized phenomenon. They do not occur uniformly across entire regions or oceans like global stressors such as ocean warming or acidification (Pratchett et al., 2017; Xiao et al., 2022). An outbreak might devastate one reef while a neighboring one remains largely untouched (Pratchett et al., 2017; Xiao et al., 2022). The drivers that trigger the outbreak—such as the localized reduction in predator populations or a sudden increase in nutrient runoff—are also confined to a specific area. **(3) Manageable at a Local Scale**. CoTS outbreaks can be managed with local intervention. Manual removal of the CoTS, culling with injections, and establishing marine protected areas to restore predator populations are all effective conservation strategies implemented at the local or regional level (Li et al., 2019; Pratchett et al., 2017). This distinguishes them from truly global stressors like ocean warming or acidification, which cannot be mitigated by any single community or nation. Therefore, although COTS themselves are a biological threat, their outbreaks are often the result of failures in local management (Skinner et al., 2025). This makes them fundamentally different from global-scale phenomena and justifies their classification as a local driver.

In our study, CoTS outbreaks are classified as a local driver. The CoTS outbreaks and their impacts are spatially confined. The evidence for their local causality in HNXS is strong: our time series data show a clear temporal alignment between a drastic drop in fish density, a CoTS outbreak, and a subsequent sudden decline in live coral coverage. This finding is consistent with the leading hypothesis of prior research, which identified a decline in CoTS predators (due to fishing) as a key local driver for an outbreak (Li et al., 2019; Pratchett et al., 2017). This substantial decline and long-term low level in fish abundance (Fig.1& Fig.S9b) is a direct result of localized overfishing from distant-water fleets and represents a critical local stressor. Fish densities have not recovered since their initial collapse, resulting in CoTS outbreaks being a periodic threat and potential isolated stressor. As recorded in 2018, CoTS outbreaks recurred in HNXS and was controlled with local interventions (manual removal of CoTS), further supporting this classification.

See lines 294: Temporal alignment between CoTS population surges **(Fig. 1c & 1f)** and coral mass mortality events **(Fig. 1c)** strongly indicates CoTS outbreaks as direct triggers of reef degradation[72,73]..

Supplementary Methods

See lines 140: The turbidity (Fig.2c, remote sensing monitoring) suspended solids variation (Fig.S10i, cruise monitoring), which represent major coastal construction impacts.

The SEM should be an easy-to-follow, effective tool to analyse the complex data and visualise the results; however many of their results appear contrary to known biological knowledge and inconsistent across regions, suggesting problems with the model structure or the analyses. For example, the positive links between SST and both macroalgae and COTs in HNXS is not based on known ecological knowledge, and the apparently strong COTS effects are not emerging from the SEM shown in Fig 3. For HNE: resident population was found with a negative effect on macroalgae, what is the biological basis for this (in HNS it is positive)? In HNS, agriculture doesn't affect turbidity or macroalgae, but in HNXS, fish densities increase turbidity? Etc.It is difficult to tell what is going on, but a separation of destructive fishing and fish densities may help here.

Response: We thank the reviewer for the detailed and helpful feedback. This observation reveals the indirect ecological effects and complexity of multi-driver systems. The different patterns result from non-linear, time-specific interactions and the endogeneity of environmental variables, all of which are captured by the SEM model. These finding are ecologically reasonable when considered within each subregion's unique baseline conditions, temporal dynamics, and multi-stressor interactions. Below we clarify the different patterns and outline the changes made to improve clarity in detail.

Model results and biological interpretation.

Our initial model was established based on a priori knowledge **(Fig. S3)** and panel analysis results to explore the direct and indirect effects of socioeconomic stressors such as agricultural N losses on LCC and assess the influence of ecological factors. And our analyses is based on within-region comparisons over time rather than across regions, which stems from disturbance regimes differ in both type and intensity in every region. This approach aligns with the tailored management under the Integrated Coast-Reef Management framework. Each regional model was fitted independently to avoid forcing a single structure on ecologically distinct systems. Variables were retained only when their inclusion improved model fit ($\Delta AIC > 2$, $p < 0.05$).

HNXS (Xisha Islands). The positive links between SST and both macroalgae and CoTS are not direct causal pathways in our model, but rather a reflection of indirect effects and the timing of disturbances. The positive SST–CoTS and SST–macroalgae links reflect a post-disturbance cascade effect: elevated SST coincides with the late phase of CoTS outbreaks that caused extensive coral mortality, with subsequent bare substrates enabling opportunistic organisms like macroalgae to proliferate. Rising and increasingly frequent SST anomalies then suppress coral larval supply and survival, while simultaneously favouring macroalgae (Hernández et al., 2018) and CoTS recruitment (Lang et al., 2017; Byrne et al., 2021). Following the initial decline of LCC, coral coverage failed to recover as a consequence of persistent environmental pressures, with rising SST as one of the primary factors (Huang et al., 2020; Kimura et al., 2022).

Thus, the SEM model likely captures that rising SST acts as a catalyst and a primary stressor in degraded reef ecosystem, creates the conditions — a low live coral cover state — and becomes a significant drivers of the ecosystem's non-recovery. The positive links reflect this indirect and complex relationship.

Population and Macroalgae. The contrasting effects of resident population (POP) on macroalgae are due to distinct local contexts and the endogeneity of environmental variables. The POP represents non-agricultural runoff and land-based pollution from coastal construction. The contrasting effects of POP on macroalgae are due to distinct local contexts **(Fig.3b & Fig.S5b)**. In HNS, a positive link reflects a direct relationship where POP sharply growth is tied to increased land-based pollution and no-agricultural nutrient input, which fuels macroalgal proliferation. In HNE, however, the overall POP shows a slow, fluctuating growth trend and it's urbanization process driven by large-scale rural-to-urban population. The model's negative link here suggests that this demographic shift is a proxy for positive local management efforts. These actions, though not directly captured by POP numbers, may include urbanization-driven internal migration or small-scale conservation efforts (e.g. environmental infrastructure expansion keeps pace with gradual population growth) **(Fig.3b & Fig.S5a - c)**, which help mitigate macroalgae growth. We have expanded these points in the discussion **(lines 242-251, 263-266)** to clarify how local drivers operate in HNE and HNS.

Agricultural N and Turbidity/Macroalgae. In HNS, agricultural N has no significant effect because its nutrient output is not a primary driver of nutrient enrichment or turbidity in the coastal waters (Gou et al., 2017; Shi et al., 2010). The limited magnitude of agricultural N increase means it is not the main contributor to the long-term changes observed in macroalgae.

Fish Density and Turbidity. Our analysis shows a positive link between fish density and turbidity in HNXS. This is not a contradiction. This constrained response reflects favorable water quality characterized by low nutrient levels and high transparency in the HNXS, likely due to minimal land-based pollution in remote reefs. In remote reefs, the ecological basis is that a significant decrease in fish density **(Fig.1e)** and reef structure complexity (Graham et al., 2013), particularly benthic feeders, leads to a reduction in bioturbation and resuspension of sediments, resulting in clearer water (Carneiro et al., 2021; Rogers et al., 2014).

Ultimately, these findings highlight the impact of a stressor is highly context-dependent and can manifest in non-intuitive ways as an ecosystem changes. And the SEM provides a more nuanced, ecologically grounded understanding of how diverse stressors interact and influence reef health in a given region.

A separation of destructive fishing and fish densities.

We appreciate the reviewer's suggestion regarding the differentiation of fishing impacts. As replied to the previous second question, it is difficult to separately record destructive fishing (blast and cyanide) and overfishing (fishing nets and traps) from field surveys. Precise and long-term quantification to separate these dynamic activities is challenging. To address this challenge, we compiled a comprehensive dataset of four fishing indicators, including data from the Global Fishing Watch (GFW), the number of fishing vessels, fishing production, and fish density **(in Fig. S8)**. After rigorous data screening, only fish density was found to meet the necessary statistical criteria for inclusion in our final models. Both forms of fishery activities are loaded on the same latent variable-fish density in this study **(Fig. 1e)** and cannot be disentangled statistically without over-parameterising. The other three indicators **(Fig. S8)** were also retained as crucial supporting data to corroborate our findings, thus enhancing the overall confidence in our results of fishing stressor.

See lines 242-251: From 2000 to 2020, the POP in Hainan East exhibited a slow, fluctuating growth trend (average annual growth rate <1%, range from 491,391 to 547,400). And the urbanization rate escalated from 18.5% in the 2000s to 55% in 2020, accompanied by an urban population increase of ~210,000 compared to a dramatic rural decline of ~150,000 **(Fig. 3b & Fig. S5c)**. The urbanization process in

Hainan East was primarily driven by large-scale internal migration of rural-to-urban population **(Fig. S5c)**, which distances human activity centers from coastal reefs[10] and reduces disturbances to ecosystems (e.g. centralizing domestic wastewater treatment). The relatively stable and low annual domestic sewage discharge in Hainan East over the past two decades (Fig. S5d) further demonstrates that this slow-growth, internally driven urbanization can aid control pollution, as environmental infrastructure expansion keeps pace with gradual population growth.

See lines 263-266: Driven by large-scale external migration, this urbanization might cause urban expansion to outpace the development of environmental infrastructure (e.g., wastewater treatment), as evidenced by the rapid increase in domestic wastewater generation in Hainan South **(Fig. S5d)**.

Finally, the model results (in Fig 5) suggest the improvement of coral cover given region specific tailored management action based on land-based interventions, such as nutrient reduction, fishing quotas, and CoTS control. Would it be more informative to show a matrix of all three main management actions at disposition for all three regions? At present, the case study 1 mixes up nutrients and COTs removal, why?

Regions	Live coral coverage (Mean (Range))		Management Paths
	Actual trends (baseline)	Optimal Management	
HNE	11.86% (3.00~31.00%)	26.44% (12.02~63.34%)	Nutrient reduction (0.6 folds) + Fishing control and increasing fisheries resource (1 folds)
HNS	18.04% (1.50~43.00%)	31.17% (3.97~87.51%)	Nutrient reduction (0.5folds) + Fishing control and increasing fisheries resource (1 folds)
HNXS	5.15% (1.15~21.25%)	28.08% (15.15~37.73%)	Fishing control and increasing fisheries resource (>250 ind/100m²)

Note: This case that represents an integrated, optimal management scenario for each region, combining the most effective interventions identified in our models to keep more than10% live coral coverage on reefs.

Response: We thank the reviewer for this constructive suggestion. We agree that a matrix would provide a clearer overview of the management actions. We have added more information to explicitly show a matrix of all three main management actions in **Fig. 5g**, Methods and Supplementary Information **(Table S6)**.

We have also added more explanation on the combination of nutrient reduction in some regions and CoTS removal in another within Hypothetical Case 1. We aim to identify a single and dominant management intervention across the relevant subregions for each hypothetical case. To clarify our analytical approach, we have restructured the hypothetical cases as follows:

Hypothetical Case 1 (HC1): Nutrient Reduction. This case now exclusively focuses on the reduction of land-based nutrient emissions in subregions where nutrients were a key stressor (HNE and HNS).

Hypothetical Case 2 (HC2): Fisheries Management. This case now exclusively models the effect of increasing reef fish density through enhanced fisheries management in all three subregions.

Hypothetical Case 3 (HC3): CoTS Removal. This case now focuses solely on the projected removal of Crown-of-Thorns Starfish (CoTS) in the HNXS subregion, where CoTS was identified as a critical driver.

Hypothetical Case 4 (HC4): Optimal Management. This case represents an integrated, optimal management scenario for each region, combining the most effective interventions identified in our models.

We have revised in the Methods (**Lines 553-580**). This revised structure allows us to more clearly and robustly compare the individual contributions of each management action and to present an integrated solution.

See lines 553-580:

Hypothetical Case 1 (HC1). Nutrient Reduction. This case exclusively focused on the reduction of land-based nutrient emissions in subregions where nutrients were a key stressor (Hainan East and Hainan South). Specifically, building on actual trends from 2011 to 2020, we assumed that there was a 60% reduction in nutrient (nitrogen) emission from land into waters in Hainan East and Hainan South, equivalent to those of the 1990s. For Hainan East, livestock and crop subsystems were projected to decrease 50% of agricultural nutrient discharge to waters, aquaculture subsystems were projected to decrease 90% of agricultural nutrient discharge. For Hainan South, 50% of nutrient discharge to waters could be reduced from agricultural green development. For Hainan Xisha, there was no typical land-based stressors, so nutrient reduction measures were not currently required.

Hypothetical Case 2 (HC2). Fisheries Management. This case exclusively modeled the effect of increasing reef fish density through enhanced fisheries management in all three subregions. Specifically, based on actual trends from 2011 to 2020, we assumed that there was a one-fold increase in coral fish density in Hainan East, Hainan South and Hainan Xisha during 2011 to 2020. The improvement of fishery resources through releasing of fish seeds, enforcing the restricted fishing areas and closed periods were projected to increase reef fish density by one-fold, where coral fish density was higher (e.g. 50 ind/100m^2) while nutrient pollution remains high.

Hypothetical Case 3 (HC3). CoTS Removal. This case focused solely on the projected removal of CoTS in the HNXS, where CoTS outbreaks was identified as a critical driver. For Hainan Xisha, the removal of CoTS was projected in 2011-2020, where the CoTS abundance was lower, and coral fish density remains low. For Hainan East and Hainan South, there was no CoTS outbreaks, so CoTS removal measures are not currently required.

Hypothetical Case 4 (HC4). Optimal Management. This case represented an integrated, optimal management scenario for each region, combining the most effective interventions identified in our models. For Hainan East and Hainan South, integrated coast-reef management scenarios have been implemented. For Hainan Xisha, the improvement of fishery resources through building no-take marine reserves and enforcing the Summer Fishing Ban were projected to increase reef fish density to 250~300 ind/100m^2.

Reviewer #2 (Remarks to the Author):

Summary

This paper leverages a long-term data set (1990s to 2020) for the northern South China Sea to identify key drivers for coral cover decline in the region. Through regressions and structural equation modeling, the authors find that local anthropogenic stressors are collectively stronger predictors for live coral cover than climate associated drivers. Additionally, the authors perform simulations to test the effects of hypothetical mitigation scenarios on live coral cover in the region.

Response: We appreciate your positive evaluation of our manuscript and the constructive comments that have significantly enhanced its quality.

Major comments

I think this paper has potential. The major finding of this paper—that local stressors are collectively more important than global stressors—is important and timely. There is a growing body of literature showing that local stressors can have significant effects, but from my understanding that literature does not necessarily claim that local stressors are more important. This paper highlights the importance of mitigating local stressors for coral conservation. I also appreciate that this study is focused on a region that is relatively understudied for coral reefs systems. With careful attention to improving readability and clarifying key concepts, this study could be a key contribution to the literature connecting various stressors to coral cover.

Response: We thank the reviewer for recognizing the significance of our regional focus and the practical implications of local stressor mitigation. We have reorganized the text to improve readability and clarity of some key concepts. For example, reducing the use of abbreviations, rewriting lines 185-193 in the Results and Discussion, and rewriting lines 442-448 in the Materials and Methods (see the point-by-point responses to your comments in the Line edits section below).

Minor comments

With that being said, I found this paper quite hard to follow for a couple of primary reasons that the authors should carefully address. First, there is an excessive use of acronyms. I think the authors should try to use acronyms as sparingly as possible. For example, I don't think it necessary to shorten 'live coral cover,' 'South China Sea,' 'Integrated Coast-Reef Management,' etc. I know that the sites (HNE, HNS) sometimes refer to several regions, but I think renaming those to something like 'Hainan East' and 'Hainan South' would greatly improve readability. Second, there were some incomplete or vague sentences throughout that need to be fixed. Several conclusions also appear to overstate what can be reasonably inferred from the results. I will do my best to point these out in the **Line Edits section**.

Response: We thank the reviewer for the thorough review of the manuscript. Following the suggestions, we have reduced the use of acronyms , such as 'South China Sea,' 'Integrated Coast-Reef Management,' 'Hainan East' and 'Hainan South' (see revised manuscript and new original text). The term 'agricultural N' has also been unified throughout the manuscript (**see the Line edits section**).

In terms of key concepts that need clarification, the authors need to fully explain how tourism was quantified. Lastly, I read through the Supporting Information and the approach for evaluating the hypothetical scenarios was not explained. Was the structural equation model used?

Response: Thank you for your valuable suggestion. We have added relevant clarification in the Materials and Methods '**Data on socio-economic drivers of coral coverage change'** section of the Supporting Information.

See lines 537-541: "According to tourist surveys, the percentage of tourists staying in Hainan was 40.3% for 3 days, 31.2% for 7 days, 25.6% for 14 days, and 2.9% for >14 days[89,90]. The number of overnight tourists travel each year were converted to resident population according to the formula $Y_{T\_POP} = X_{POP} + X_{tourists} * (0.403 * 3 + 0.312 * 7 + 0.256 * 14 + 0.029 * 21) / 365$ (the details see the Supplementary Methods)."

For the hypothetical scenarios evaluation, the predictive results of scenario analysis are based on structural equation models. We also have added relevant clarification in the Materials and Methods '**Hypothetical cases for the past and alternative scenarios**':

See line 548: "Based on the Integrated Coast-Reef Management framework, we estimate live coral coverage from land-sea management scenarios in the typical subregions under different hypothetical cases for 2011–2020 **using the SEM**."

Line edits

General note: Fix the term "agriculture N" to "agricultural N" throughout the manuscript

Done.

70: Suggest removing 'being'

Done.

79: Change 'industry' to 'industries'

Corrected.

80: missing part of sentence after 'areas'; inappropriate expansion of what?

Corrected.

See lines 80-84: Overdischarge of nutrient is one of the main factor that connects human behaviors with degradation of tropical coastal reef. Inappropriate **agricultural expansion and tourism infrastructure development (e.g., coastal hotels and sewage systems)** drive nutrient leakage into coastal ecosystems.

88: Further improvement in terms of or relative to what exactly? Do you mean that new approaches have been developed?

Response: The wording was indeed ambiguous, and we have revised it for clarity. By "further improvement," we are referring to the advancement from traditional single-factor analyses to more sophisticated statistical approaches capable of modeling complex, multi-causal relationships. For example, new approaches such as Bayesian modelling, Panel regression and Structural Equation Modeling (Xu et al., 2022). These methods allow us to test and quantify the direct and indirect effects of multiple interacting stressors simultaneously, which is crucial for a more holistic and robust identification of the most critical drivers of coral reef decline.

See lines 91-93: Additionally, there is further improvement in the mathematical analysis of driver interactions and multi-causality (e.g. credibility of quantitative analysis), which has been demonstrated in the management of ecosystems in both terrestrial and marine environments, aiding in the identification of critical stressors[2,25,26].

92: If this is what you mean, I suggest rephrasing to “Focusing on the northern South China Sea, an urbanized reef hotspot, …”

Done, thank you.

See line 97: Focusing on **the northern South China Sea,** an urbanized reef hotspot, this study leverages two decades of systematic monitoring across 102 sites spanning 22 reefs in the northern South China Sea to quantify multi-stressor impacts on live coral coverage (LCC) through a coupled land-sea systems approach.

96: What does telecoupled mean?

The text of this sentence has been reorganized. ‘telecoupled’ means that telecoupling analysis (distal human ones and reefs) explicitly models socioeconomic-ecological interactions across regional or local reefs (Hovis et al., 2021; Hull et al., 2019). In the context of of integrating prior knowledge, applying the telecoupling framework to coral reefs would involve explicitly analyzing how distal socioeconomic factors, such as human gravity, tourism, markets consumption, or agriculture development, affect the local ecological conditions of a specific reef (Hughes et al., 2017; Fig. S3a).

See line 101: “We employ panel regressions and structural equation modeling (SEM) to **perform telecoupling analysis**[2] and identify the main drivers of LCC change, ...”.

106: Missing part of the sentence?

Corrected. The text of this sentence has been reorganized.

See line 106: "Based on the results, we further propose an Integrated Coast-Reef Management (ICRM) framework with tailored strategies to improve coral reef resilience under ocean warming, more generally, enable prioritization of ecological interventions for reef management. **To empirically validate intervention efficacy, we implemented scenario analyses leveraging our best structural equation modeling.** Importantly, our scenario analyses, which consider the interactions and cascading effects of multiple stressors within the ICRM framework, assess whether and how prioritizing interventions under climate warming could be effective in recovery of degraded reefs."

107: "in an anthropogenically"

Corrected, thank you.

See line 114: This systemic approach contributes a paradigm shift from reactive conservation to predictive, stressor-specific management **in an anthropogenically** complex reef system.

118: This is an example of excessive acronyms that make the paper very difficult to follow for an unfamiliar reader.

Thank you for this suggestion. We have reduced the use of acronyms, for example, renaming 'HNE' and 'HNS' to 'Hainan East' and 'Hainan South'.

122: Change to coral reefs

Corrected.

See line 128: "Local stressors outpace climate warming impacts on coral **reefs.**"

148-150: These references seem to be regionally constrained to South China Sea, so I suggest modifying this sentence to reflect that.

Done, thank you.

See line 157: "Our quantitative results confirm previous qualitative studies [30,31], suggesting that the loss of LCC could be more vulnerable to local anthropogenic disturbances rather than climate change-induced ocean warming and typhoons in **the South China Sea.**"

177: This is a potential/plausible mechanism that I don't think is directly supported by this study. I suggest adding "fishing COULD initiate a critical …"

Done, thank you.

See line 182: "The depletion of LCC induced by destructive fishing **could initiate** a critical threshold response: deteriorating reef architecture diminishes niche diversity and larval recruitment success, creating an autocatalytic degradation process that progressively erodes ecosystem resilience."

163-183: This entire last section should be written so that it's clear that these are your hypotheses/interpretations of your findings.

Corrected, thank you. The text of this entire paragraph has been reorganized.

See lines 171-193: "The dual regulatory effects of human activities on both top-down and bottom-up processes in coral reef ecosystems demonstrate clear spatial heterogeneity in this region, modulated by subregional environmental characteristics and connectivity between ecosystems[43,44]. Our analyses identify unsustainable fishing practices as the predominant local driver of reef degradation, evidenced by sustained declines and low levels in fish densities across all surveyed regions. The underlying mechanisms encompass overfishing, habitat damage, and direct coral mortality resulting from destructive fishing practices (e.g., blast and cyanide fishing)[29,45]. The SEM analysis reveals a significant and direct impact of fish density on LCC, while also intensifying the effect indirectly through the regulation of macroalgae or CoTS abundance. Cumulatively, fish density explained 27.50% to 44.90% of LCC variation in three typical subregions (Fig. 3a). The impact of fish on LCC remains the highest, even when land-based disturbances are considered. These unsustainable fishing activities had been observed frequently in various reefs in the South China Sea through the 20th century[30,46,47], leading to a decline in both coral reef fish density and species diversity[48] (Fig. 1e) and even mass coral mortality[49,50]. **Reef fish plays a pivotal role in the biogeochemical cycling and trophic dynamics of coral reefs. For instance, healthy predatory relationships and their excrement can enhance primary productivity, promote coral growth and regulate trophic ratios in reef ecosystems[51]. The reductions of reef fish density and species diversity can destabilize food webs, which in turn affects the balance and biodiversity of the entire ecosystem[29]. Taken together, the coral reef degradation observed is consistent with the threshold cascade hypothesis. That is, the depletion of LCC induced by destructive fishing could initiate a critical threshold response: deteriorating reef architecture diminishes niche diversity and larval recruitment success, creating an autocatalytic degradation process that progressively erodes ecosystem resilience.**"

201: Change 'agriculture nutrients inputs overload' to 'agricultural nutrient inputs' or similar

Corrected.

203: Remove 'in HNE'

Done.

206: Remove 'a part of'

Done.

208: change 'agriculture' to 'agricultural'

Corrected.

219: change 'enhances' to 'enhancing'

Corrected.

225: Hysteresis is a specific mathematical pattern that your study does not directly show. Suggest stating "potentially leading to hysteresis in reef …"

Done, thank you.

See line 237: This dual degradation pathway—reduced top-down control and enhanced bottom-up enrichment—**potentially lead to** hysteresis in reef recovery, as macroalgae dominance suppresses coral recruitment and alters biogeochemical cycling.

230: Incomplete sentence

Corrected. The text of this sentence has been reorganized.

See line 246: "The urbanization process in Hainan East was primarily driven by large-scale internal migration of rural-to-urban population (Fig. S5c), which distances human activity centers from coastal reefs[10] and reduces disturbances to ecosystems (e.g. centralizing domestic wastewater treatment)."

252: Remove 'with'

Done, thank you.

255: Make sure to explain how you are dealing with tourism

Done, thank you. We have added relevant clarification in the Materials and Methods '**Data on socio-economic drivers of coral coverage change'** section of the Supporting Information.

See lines 537-545: "According to tourist surveys, the percentage of tourists staying in Hainan was 40.3% for 3 days, 31.2% for 7 days, 25.6% for 14 days, and 2.9% for >14 days[89,90]. The number of overnight tourists travel each year were converted to resident population according to the formula $Y_{T\_POP} = X_{POP} + X_{tourists} * (0.403 * 3 + 0.312 * 7 + 0.256 * 14 + 0.029 * 21) / 365$ (the details see the Supplementary Methods)." T_POP is the resident Population (T_POP), including overnight tourists travel were converted to resident population per year, denotes local urban development gravity - an indicator of nearby human settlements potential influences on coral reefs (e.g., water quality and land use)."

272: Change 'outbreak' to 'outbreaks'

Corrected.

279: Change 'predators' to 'predator'

Corrected.

286: 'in the food chain'

Corrected.

290: Change 'reefs' to 'reef'

Corrected.

298: Incomplete sentence

Corrected. The text of this sentence has been reorganized.

See line 321: The Integrated Coast-Reef Management framework provides tailored paths **to** local coral reef governance (Fig. S9 & Table S5), **supporting** the fulfillment of United Nations Sustainable Development Goals (SDG 14) and Decade of Ocean Science priorities.

309: Not sure if MC is defined but I think these factors should all be spelled out

Done, thank you. MC denotes macroalgae coverage, the first abbreviation of MC has been added with an explanation.

See Figure 4 and line 103: "We employ panel regressions and structural equation modeling (SEM) to perform telecoupling analysis[2] and identify the main drivers of LCC change, including abiotic factors (e.g., sea surface temperature, turbidity, typhoon), biotic factors (e.g., fish, **macroalgae coverage (MC)**, CoTS abundance, coral species richness), socio-economic factors (e.g., urban sprawl, agriculture development), as well as their interactions. Within this, agriculture development dynamics are quantified via tracing nutrient flows and losses."

310: Incomplete sentence

Corrected, thank you. The text of this sentence has been reorganized.

See Lines 332-334: "Hainan Xisha reefs exhibit low resilience, **characterized by mean LCC <10% and MC/LCC <1/3,** combined with excessive fishing pressure surpassing ecological function thresholds."

322: Change 'considering' to 'under'

Corrected.

347: "could be more helpful"?

Corrected.

356: Change 'has' to 'have'

Corrected.

373-386: To me, this reads more like a Conclusions/Summary section rather than Conservation Implications. Suggest changing the subheading or re-writing or re-organizing this paragraph to be more about Conservation Implications.

Done, thank you, the subheading has been corrected with "**Conclusions**".

407: Change 'transplant' to 'transplantation'

Corrected.

415: What do you mean by sieving?

We also have added relevant clarification in the Materials and Methods "**Coral reef data.**" The 'sieving' criteria is that the coral reef have at least five consecutive years of monitoring data.

See Lines 449-452: "**After filtering (based on the condition that each reef should have at least five consecutive years of monitoring data)**, this dataset includes the LCC for 22 reefs across 3 subregions over two decades (Fig. 1)."

418: What is (remove)?

Corrected. "remove" refers to the discrete data from coral reef survey being removed when conducting quantitative driver analysis (panel and structural equation modeling).

See line 445-446: "Data of the annual monitoring survey were then binned between long-term successive and discrete types, with discrete data excluded from quantitative driver analysis."

418: What do you mean by reef check survey and by simple random sample survey? please elaborate

We also have added relevant clarification in the Materials and Methods "**Coral reef data.**" The 'reef check survey' means a comprehensive survey for the entire reef zones; 'simple random sample survey' means that sampling monitoring, some sites are randomly selected from all sites.

See line 447-448: "For each coral reef, a coral reef survey (comprehensive survey monitoring) or simple random survey (sampling monitoring) is conducted annually, with at least 3 sites per reef for simple random sample surveys."

432-443: This paragraph is written in present tense while the previous paragraphs were written in past tense.

Corrected. This paragraph (lines 540-454) has been rewritten in the past tense.

We thank the reviewer for highlighting the grammatical inconsistency. The Materials and Methods section has been comprehensively revised to uniformly apply the past tense for all research actions (e.g., data analysis, model fitting), while retaining present tense only for universal definitions and software properties.

440: Change 'dynamics' to 'dynamic' and 'agriculture' to 'agricultural'

Corrected, thank you.

464: "through an ordinary least squares"

Corrected, thank you.

475: "Beta_k is the estimated coefficient" and "gamma is the spatial autoregressive coefficient"

Corrected, thank you.

479: construct piecewise structural… OR conduct piecewise structural equation modeling

Corrected, thank you.

491: Incomplete sentence (starting "our initial model")

Corrected. The text of these three sentences has been reorganized.

See line 528-533: "Our initial model was established based on a priori knowledge (Fig. S3) and panel analysis results to explore the effects of coral reef fishery resources, water quality and human activity factors on the LCC. Using the d-sep test, we add missing paths step-by-step to construct a set of candidate SEMs. We select the model with the lowest AIC value as the best model and calculated the direct, indirect, and relative total effects on establishment success (Table S4)."

492: Change "result" to "results"

Corrected.

502: What does keep more than 10% mean?

Response: It has been found that when less than 10% of the threshold of live hard coral cover, coral reefs are more likely to exhibit a neutral or negative carbonate budget and may suffer from coral reef submersion due to sea level rise (Perry et al. 2018). And previous studies have identified 10% hard coral cover as a minimum threshold for carbonate production on Indo-Pacific reefs (Januchowski-Hartley, et al. 2017; Perry et al. 2016).

We also have added relevant clarification in the Materials and Methods '**Hypothetical cases for the past and alternative scenarios**'.

See line 550-551: "Three cases were developed to compare the contribution of the various drivers on the increase in LCC to keep it above 10% in most reefs - **a threshold required for carbonate production on reefs**[22] (Table S5)."

References

Brüderl, Josef, and Volker Ludwig. "Fixed-effects panel regression." The Sage handbook of regression analysis and causal inference 327: 357 (2015).

Zulfikar, Rizka, and M. M. STp. "Estimation model and selection method of panel data regression: An overview of common effect, fixed effect, and random effect model." JEMA: Jurnal Ilmiah Bidang Akuntansi 9.2: 1-10 (2018).

Taşdemir, Industrialization, servicification, and environmental Kuznets curve: non-linear panel regression analysis. Environ Sci Pollut Res 29, 6389–6398 (2022). https://doi.org/10.1007/s11356-021-16012-9

Li, X. et al. Coral community changes in response to a high sedimentation event: A case study in southern Hainan Island. Chinese Science Bulletin. 58, 1028-1037 (2013).

Xing Shuai, Tan Yehui, Zhou Linbin, et al. The influence of water turbidity on symbiotic zooxanthellae of different reef-building coral species [J]. Chinese Science Bulletin, 57(5):7 (2012).

Sully S, van Woesik R. Turbid reefs moderate coral bleaching under climate-related temperature stress[J]. Global Change Biology, 2020, 26(3): 1367-1373.

Zweifler A, O'leary M, Morgan K, et al. Turbid coral reefs: past, present and future—a review[J]. Diversity, 2021, 13(6): 251.

Li, X. et al. Spatial and temporal variations in sediment accumulation and their impacts on coral communities in the Sanya Coral Reef Reserve, Hainan, China. Deep Sea Research Part II: Topical Studies in Oceanography. 96, 88-96 (2013).

Guo, J. et al. Nutrient Distribution in Coral Reef Degraded Areas within Sanya Bay, South China Sea. J. Coast. Res. 33, 1148 (2017).

Houk, P. et al. Nutrient thresholds to protect water quality and coral reefs. Mar. Pollut. Bull. 159, 111451 (2020).

Precht, W. et al. Non-random timing of ecological shifts on Caribbean coral reefs suggests regional causes of change. Cold Spring Harbor: Cold Spring Harbor Laboratory Press; https://go.exlibris.link/NjyYG0rh. (2019).

Pratchett, M.S.; Caballes, C.F.; Wilmes, J.C.; Matthews, S.; Mellin, C.; Sweatman, H.P.A.; Nadler, L.E.; Brodie, J.; Thompson, C.A.; Hoey, J.; et al. Thirty Years of Research on Crown-of-Thorns Starfish (1986–2016): Scientific Advances and Emerging Opportunities. Diversity 2017, 9, 41.

Xiao J, Wang W, Wang X, et al. Recent deterioration of coral reefs in the South China Sea due to multiple disturbances[J]. PeerJ, 2022, 10: e13634.Lang B J, Caballes C F, Uthicke S, et al. Impacts of ocean warming on the settlement success and post-settlement survival of Pacific crown-of-thorns starfish (Acanthaster cf. solaris)[J]. Coral Reefs, 2023, 42(1): 143-155.

Byrne M, Deaker D J, Gibbs M, et al. Juvenile waiting stage crown - of - thorns sea stars are resilient in heatwave conditions that bleach and kill corals[J]. Global Change Biology, 2023, 29(23): 6493-6502.

Hughes, T. P. et al. Coral reefs in the Anthropocene. *Nature*. **546**, 82-90 (2017).

Huang H. et al. Report of the Situation of Chinese Coral Reef 2019: Pacific Society of China, Branch of Coral Reef; (2020) .

Kimura T., Chou L.M., Huang D., Tun K., Goh E. (Editors). Status and Trends of East Asian Coral Reefs: 1983-2019. Global Coral Reef Monitoring Network, East Asia Region. (2022).
Carneiro, Miguel, and Rogélia Martins. "Destructive fishing practices and their impact on the marine ecosystem." Life below water. Cham: Springer International Publishing, 2021. 1-11.
Graham, Nicholas AJ, and Kirsty L. Nash. "The importance of structural complexity in coral reef ecosystems." Coral reefs (2013): 315-326.
Rogers, Alice, Julia L. Blanchard, and Peter J. Mumby. "Vulnerability of coral reef fisheries to a loss of structural complexity." Current Biology 24.9 (2014): 1000-1005.
Hernández, Celso A., et al. Macroalgal response to a warmer ocean with higher CO_2 concentration. *Marine Environmental Research.* 136, 99-105 (2018).
Skinner C, Bozec Y M, Fletcher C S, et al. Maximising the benefits of local management for coral reefs amidst near-term environmental change[J]. Journal of Environmental Management, 2025, 392: 126627.
Li Y. C., Wu Z. J., Liang J. L., Chen S. Q., Zhao J.M. Analysis on the outbreak period and cause of Acanthaster planci in Xisha Islands in recent 15 years (in Chinese). Chin. Sci. Bull. 64, 3478-3484 (2019).
Shi Q., Zhao M. X., Huang L. Y., Yan H. Q., Zhang H. L., Human Activities and Impacts on Coral Reef at the Luhuitou Fringing Reef, Sanya (in Chinese). Tropical Geography. 30, 486-490 (2010).
Xu, M. et al. Exotic fishes that are phylogenetically close but functionally distant to native fishes are more likely to establish. Glob. Change Biol. 28, 5683-5694 (2022).
Hovis, C. L., Dou, Y., Herzberger, A., & Liu, J. Through the lens of telecoupling and metacoupling: New perspectives for global sustainability. *Sustainability*, 13(5), 2953. (2021).
Hull, Vanessa, Christian J. Rivera, and Chad Wong. "A synthesis of opportunities for applying the telecoupling framework to marine protected areas." *Sustainability* 11.16: 4450. (2019).
Shan X, Bai Z, Ma L, et al. Mitigation of greenhouse gas emissions and nitrogen losses caused by migration and tourism in China's tropical island cities[J]. Journal of Environmental Management, 393: 127054 (2025).
Chen H. and Li. L. A Study on the differentiation of tourists' stay length in Hainan. (in Chinese). Journal of Guizhou Commercial College. (2012).
Januchowski-Hartley, F. A., Graham, N. A. J., Wilson, S. K., Jennings, S. & Perry, C. T. Drivers and predictions of coral reef carbonate budget trajectories. Proc. R. Soc. B 284, 20162533 (2017)
Perry, C. T. et al. Loss of coral reef growth capacity to track future increases in sea level. Nature 558, 396–400 (2018)
Perry, C. T. et al. Remote coral reefs can sustain high growth potential and may match future sea-level trends. Sci. Rep. 5, 18289 (2016).
Perry, C. T. et al. Caribbean-wide decline in carbonate production threatens coral reef

growth. *Nat. Commun*. 4, 1402 (2013)