

# Impacts of local anthropogenic stressors outpace those of climate on coral reef collapse in the northern South China Sea

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Coral reefs are declining globally, but region-specific drivers of degradation remain poorly quantified, hindering local conservation policymaking. By collecting two decades of field data from 102 sites across 22 coral reefs in the northern South China Sea and employing panel regressions and structural equation modeling, we identify key stressors that are responsible for 40% (17–50%) of the declines in live coral cover. Local anthropogenic stressors—overfishing, nutrient pollution from agriculture and coastal urbanization—collectively explain 73% of live coral coverage variance, outweighing climate-associated thermal stress. We then propose an Integrated Coast-Reef Management framework that couples land-sea interventions—prioritizing sustainable fisheries, watershed nutrient management, and controls of crown-of-thorns starfish outbreaks. Spatial simulations indicate that this synergistical strategy could elevate live coral coverage by two to four times under global warming scenarios, avoiding reef calcification collapse. Our findings contribute to coral conservation paradigms by highlighting tailored strategies at the local level beyond globalized approaches, which offer scalable solutions for regions facing similar pressures.

Coral reefs are the most socio-economically valuable marine ecosystems and have the highest biodiversity on earth<sup>1</sup>. However, coral habitats are experiencing rapid degradation due to increasing global and local stresses from climate change and human activities<sup>2</sup>. Global coverage of live reef-building coral is estimated to have decreased by 50% since the 1950s<sup>3</sup>. The widespread loss of live corals can lead to detrimental cascade effects, including declines in reef structural complexity, fish diversity and abundance<sup>4,5</sup>, and diminishing ecosystem services from coral reefs<sup>6</sup>. Such transformations can greatly impact coastal communities that rely on coral reefs for sustenance, particularly in developing nations<sup>7,8</sup>. Therefore, it is crucial to identify

the stressors and develop adaptive management strategies to enhance reef resilience under climate warming, while minimizing negative environmental impacts and enhancing coastal sustainability for future generations<sup>9</sup>.

The rates of coral reef degradation and loss vary with geographic location and specific environmental stresses<sup>10,11</sup>. Threats to coral reefs include local stressors such as overfishing, typhoon, crown-of-thorns starfish (CoTS), tourism, terrestrial pollution, and coastal exploitation<sup>12,13</sup>, as well as global stressors<sup>2</sup> such as ocean warming and acidification, aggravated by extreme climate events<sup>14,15</sup>. Notably, 61% of reefs worldwide experience superimposed local and global stressors<sup>16</sup>,

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creating nonlinear ecological impacts that challenge predictability through altered stressors exposure intensity, organismal thresholds, and compromised adaptive capacity. Current understanding of the interactions between regional and global stressors remains limited, largely due to insufficient field data, though some research progress has been made in regions like the Great Barrier Reef<sup>17–19</sup> and Hawaii<sup>20</sup>. Critical knowledge gaps persist in urbanized reef systems where anthropogenic forcing dominates (e.g., tropical developing countries/regions). The heterogeneous nature of coral reefs, coupled with species-specific adaptations and life history traits<sup>21,22</sup>, underscores the need for region-specific studies to address multiple stressors effectively. Moreover, governance blueprints validated through stakeholder engagement remain poorly addressed.

To enhance coral reef resilience in the face of climate change and human activities, integrated land-sea management strategies are essential<sup>20</sup>. Identifying critical stressors from land to sea is crucial for effective reef conservation transitions<sup>2,10</sup>, particularly when balancing human development priorities and conservation efforts. Agriculture and tourism are the mainstay industries in tropical coastal reef areas. Overdischarge of nutrients is one of the main factor that connects human behaviors with the degradation of tropical coastal reefs. Inappropriate agricultural expansion and tourism infrastructure development (e.g., coastal tourism and sewage systems) drive nutrient leakage into coastal ecosystems. Material flow and nutrient footprint approaches, such as the NUTrient flows in Food chains, Environment, and Resource use (NUFER) model, provide valuable tools for quantifying regional-scale agriculture development by tracing nutrient flows and losses in food systems to water<sup>23,24</sup>. Unlike conventional models focusing on single sectors (e.g., croplands or livestock), NUFER's integrated approach addresses the interconnectedness of food systems (crop production, livestock production, aquaculture, and human consumption), a systemic perspective that makes it particularly effective in regions with mixed land use and intensive agriculture. 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<sup>2,25,26</sup>. These methodologies are indispensable for developing targeted interventions and enhancing the resilience of coral reefs to local and global impacts.

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. We employ panel regressions and structural equation modeling (SEM) to perform telecoupling analysis<sup>2</sup> 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), socioeconomic factors (e.g., urban sprawl, agriculture development), as well as their interactions. Within this, agricultural development dynamics are quantified via tracing nutrient flows and losses in food systems using city-scale NUFER models. 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, and enable prioritization of ecological interventions for reef management. To empirically validate intervention efficacy, we implement scenario analyses leveraging our best structural equation model. 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 the recovery of degraded reefs. This systemic approach contributes to a paradigm shift from reactive conservation to predictive, stressor-specific management in an anthropogenically complex reef system.

## Results and discussion

### Live coral coverage trajectory changes

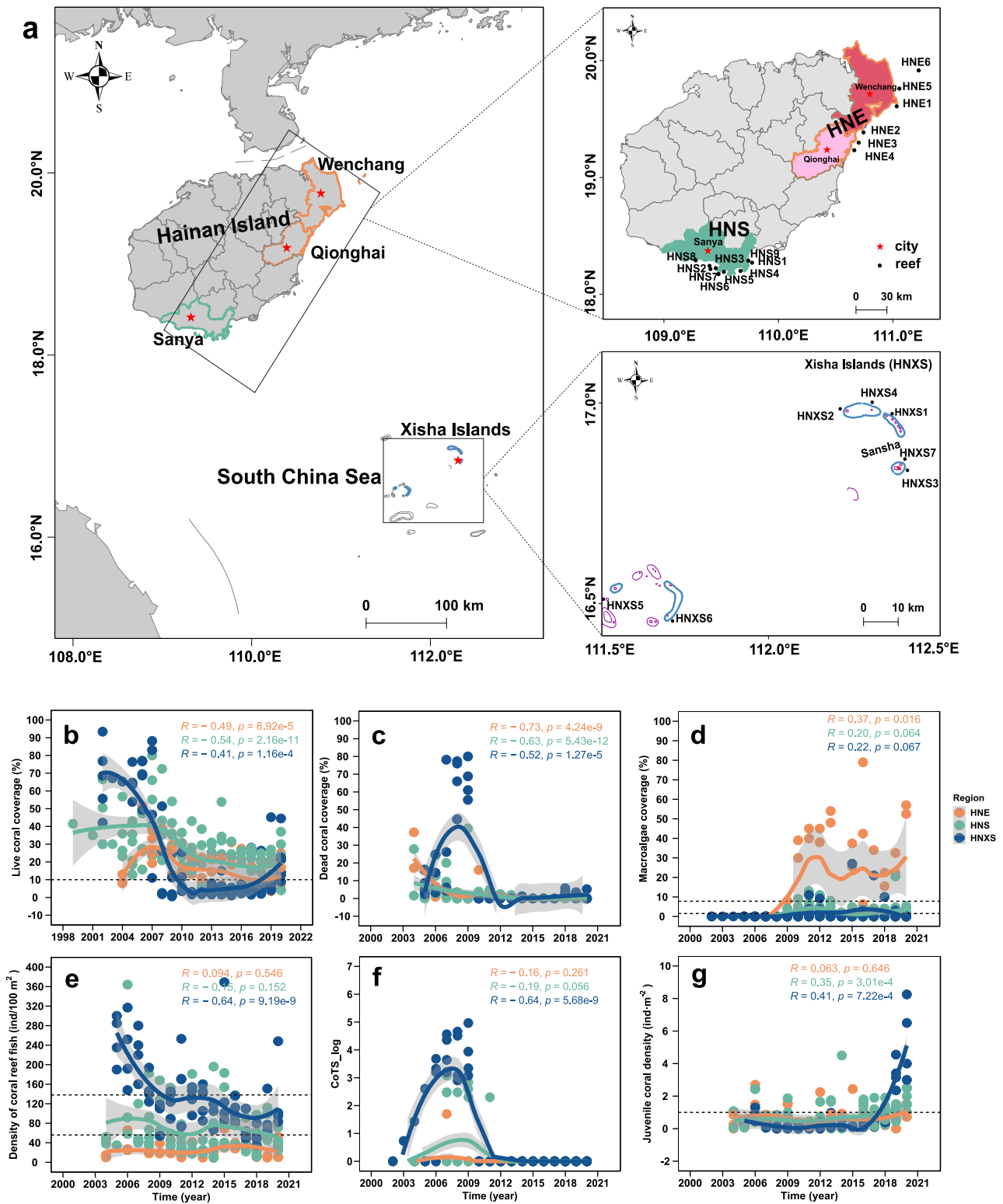
Based on the geographical characteristics and principal component analysis (PCA) of coral communities and environmental factors (Supplementary Fig. S1), coral reefs in the northern South China Sea can be clustered into three groups: Hainan East (HNE, Group 1), Hainan South (HNS, Group 2), and Hainan Xisha (HNXS, Group 3). Over the past two decades, the mean LCC across these regions declined by about 40%, with current levels averaging 19% (Fig. 1a, b). Notably, this value is lower than the average global LCC of 30%<sup>27</sup>. Subregional declines varied markedly: the average LCC in Hainan East, Hainan South, and Hainan Xisha exhibited reductions of 17, 24, and 50%, respectively (Fig. 1b). This degradation coincided with a pronounced shift toward stress-tolerant coral taxa dominance, notably *Porites* spp. (Supplementary Fig. S2), reflecting ecosystem adaptation to escalating environmental pressures.

### Local stressors outpace climate warming impacts on coral reefs

A variety of stressors interact on coral reefs and drive different ecological processes of reef degradation involving top-down (fishing), bottom-up (eutrophication), and side-in (perturbations causing direct coral mortality and habitat loss) patterns, etc.<sup>28</sup>. Based on our field surveys, we explore the regional patterns of local coral reef degradation and examine the abiotic and biotic determinants of LCC. We begin with a set of panel regressions with flexible controls of observed and unobserved factors using time and location fixed effects to explore the key factors associated with LCC, followed by the SEM analyses to pin down the direct and indirect effects of different stressors of LCC and their interactions. Consistently, both show that human activities, including fishing pressure and economic development, are the major determinants of LCC in this study.

The disturbance from fishing can be characterized by changes in fish abundance or capture fisheries production. Fishing pressure emerges as the dominant anthropogenic driver across subregions (effect size = 0.35, 0.52, 0.73, respectively; Fig. 2a and Supplementary Data 3), with reef fish density showing strong positive correlations with LCC (Fig. 2a). Specifically, a 10% decrease in fish corresponds to a 7.3, 3.5, and 5.2% reduction of LCC at Hainan East, Hainan South and Hainan Xisha in the panel regressions, respectively. Destructive fishing practices (e.g., bottom trawling or blasting fish) drive LCC loss, which subsequently reduces reef fish populations through habitat degradation, establishing a self-reinforcing cycle that perpetuates long-term ecosystem decline<sup>29</sup>. LCC is also significantly impacted by several other factors, including macroalgae, CoTS abundance, coral species composition, and SST in descending order of effect size (Fig. 2a–d), with effect sizes varying regionally. In Hainan Xisha, the decline of LCC is also directly impacted by the other factors, in descending order, including CoTS abundance ( $-0.25$ ,  $p = 3.1e-10$ , Fig. 2a and Supplementary Data 3), coral species composition ( $0.1$ ,  $p = 0.001$ , Fig. 2a and Supplementary Data 3), and macroalgae ( $-0.02$ ,  $p < 2e-16$ , Fig. 2a and Supplementary Data 3). In Hainan East and Hainan South, the panel analysis shows that fish abundance has the largest impact on LCC, followed by macroalgae (effect size =  $-0.21$ ,  $-0.48$ , respectively, Fig. 2a and Supplementary Data 3), SST (effect size =  $-0.14$ ,  $-0.25$ , respectively, Fig. 2a and Supplementary Data 3), and turbidity (Fig. 2a–c and Supplementary Data 3). Together, local biogeographical factors such as declining reef fish density, algal blooms, and CoTS outbreaks primarily explain LCC decline in the three subregions.

Our quantitative results confirm previous qualitative studies<sup>30,31</sup>, 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. This regional specificity likely stems from region-specific conditions (e.g., upwelling in Hainan East)<sup>32</sup> and/or the timing and intensity of disturbance occurrence (e.g., thermal stress) (Fig. 2d, e), and the resilience of corals



themselves<sup>33–35</sup>. Paleoclimatic records reveal the northern South China Sea endured higher temperatures and stronger El Niño events than present conditions over millennial timescales<sup>36</sup>, with recurrent historical bleaching episodes failing to drive coral extinction due to inherent resilience from species or environmental specificity<sup>37,38</sup>. Corals possess the capacity to recover from thermal bleaching (e.g., through acclimation and physiological tolerance of phenotypic plasticity) with a certain level of adaptability<sup>37</sup> subject to coral taxa, local disturbances level, and environmental circumstances<sup>39,40</sup>. Global marine heat waves

(MHWs) have become very frequent and extreme<sup>32,41</sup>, and our study areas have already experienced frequent MHWs since 2014 (Fig. 2e), indicating rising coral bleaching risks<sup>42</sup>. Given this urgency, isolating and mitigating the impacts of controllable local stressors can provide a crucial buffer time for the survival of coral reefs.

### Long-term effects of fishing stress on LCC

The dual regulatory effects of human activities on both top-down and bottom-up processes in coral reef ecosystems demonstrate clear

**Fig. 1 | The study areas and the coral community changes in the coral reefs of three subregions from 2000 to 2020.** **a** The map of study areas, including 22 reefs from three subregions in Hainan. Hainan East (HNE) denotes Wenchang and Qionghai cities located at 19° North Latitude (NL), with a yellow boundary line. Hainan South (HNS) denotes Sanya city located at 18°NL, with a green boundary line. Hainan Xisha (HNXS) denotes Sansha city located at 17°NL, with a blue boundary line. Dots on the map show reef locations; each reef consists of four to six survey sites. Basemap data obtained from the Standard Map Service website of the National Bureau of Surveying and Mapping Geographic Information (<http://bzdt.ch.mnr.gov.cn/>). **b** Live coral coverage. **c** Dead coral coverage. **d** Macroalgae

coverage. **e** Coral reef fish density. **f** The crown-of-thorns starfish (CoTS) density. **g** Juvenile coral density. **b–g** Spearman's rank correlation analysis to assess the effect of time on coral community changes for each subregion, with statistical tests conducted as two-tailed. For more statistical results, see Supplementary Fig. S10 and Data 7. Circles indicate the annual mean values for each reef from the 1990s to 2020; different colors represent different subregions, and the orange, green, and blue indicate HNE, HNS, and HNXS, respectively. **b–g** Solid lines represent the fitted lines using locally weighted scatterplot smoothing (LOESS), and the 95% CIs are shown in gray bands. The dotted lines indicate reference levels at points of abrupt change.

spatial heterogeneity in this region, modulated by subregional environmental characteristics and connectivity between ecosystems<sup>43,44</sup>. 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)<sup>29,45</sup>. 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 27.50–44.90% 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 twentieth century<sup>30,46,47</sup>, leading to a decline in both coral reef fish density and species diversity<sup>48</sup> (Fig. 1e) and even mass coral mortality<sup>49,50</sup>. Reef fish play 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<sup>51</sup>. 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<sup>29</sup>. 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.

While recent management interventions (summer fishing ban, fishing production reduction; Supplementary Fig. S8) have slowed resource declines, they remain insufficient to reverse decades of ecological debt. Current LCC and fish biomass levels persist below functional thresholds required for autonomous recovery, demonstrating the legacy effects of chronic overexploitation. Critical to rehabilitation efforts is restoring keystone fish guilds—both herbivorous and predatory fish populations must be rehabilitated to reestablish trophic control mechanisms and biogeochemical functionality<sup>52</sup>. Our decadal-scale observations underscore that conventional fisheries management alone cannot achieve reef recovery, necessitating targeted and ecosystem-based restoration strategies to complement existing conservation measures.

### High heterogeneity of regional dominant factors in coral reef degradation

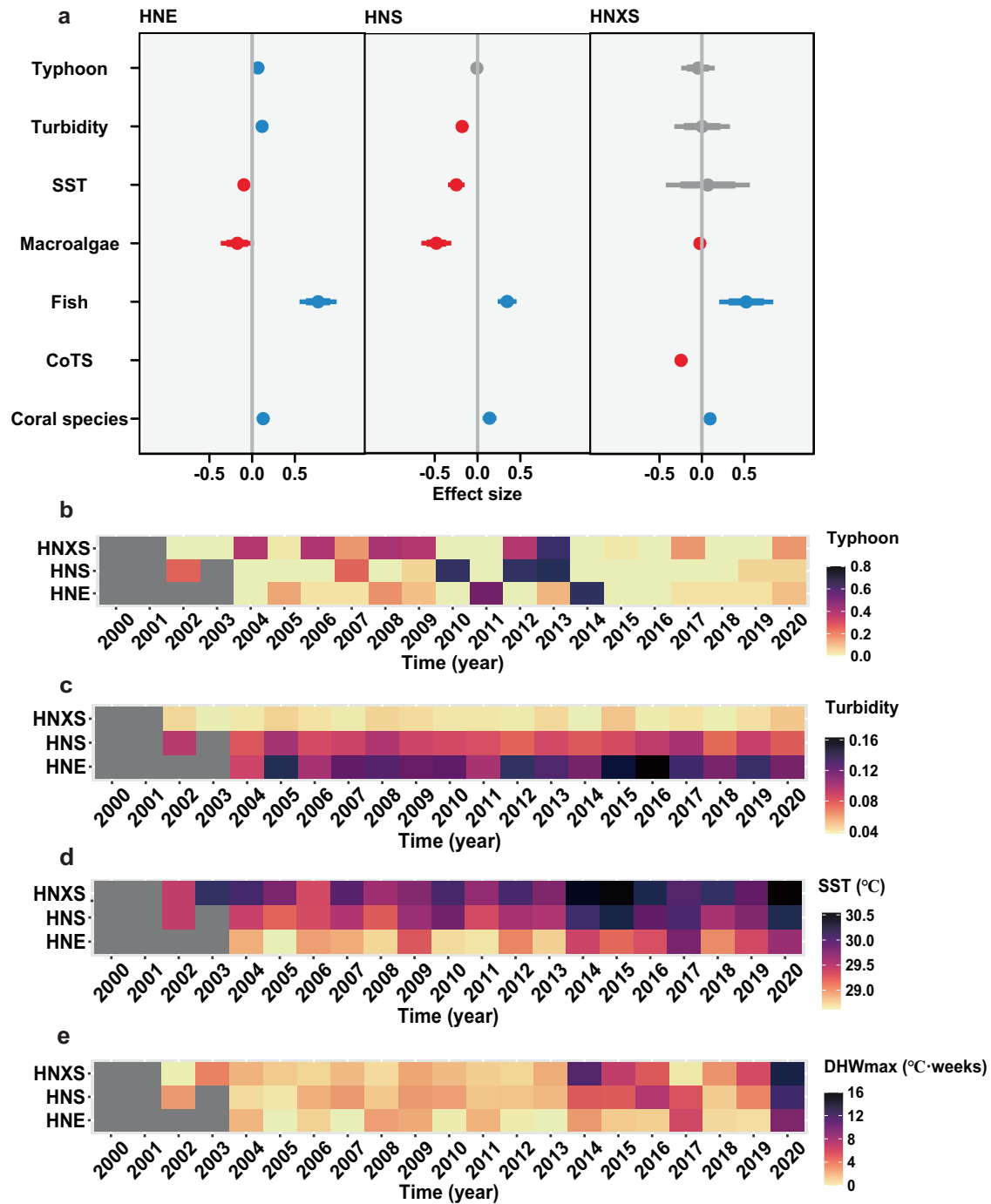
Our findings demonstrate that the LCC trajectory is governed by interacting socioeconomic factors beyond fisheries, with agriculture expansion, urbanization, and tourism collectively exacerbating land-based nutrient loading, bioerosion, and coastal habitat modification. Nearshore reefs in Hainan East and Hainan South have experienced disproportionately higher anthropogenic pressures compared to remote reefs in Hainan Xisha, reflecting differential exposure to stressors derived from regional socioeconomic development. Our results highlight the key finding that the impact of any given stressor is

highly dependent on the local ecological baseline (e.g., species composition and environmental background), the disturbance's timing and intensity, and interactions with other stressors.

### Overfishing and agricultural nutrient input induce coral-algae phase shift

In Hainan East, water eutrophication due to agricultural development has emerged as the secondary predominant mechanism leading to the degradation of coral reefs. The NUFER model analysis indicates that agricultural nutrient emissions in Hainan East have increased by over 100% from 2000 to 2020 (Fig. 3c), driven primarily by crop production (~50% contribution, Supplementary Fig. S6) and rapidly expanding mariculture (Supplementary Fig. S7). Prior to 2016, a part of mariculture effluent entered coastal waters untreated, adversely affecting nearby coral reefs<sup>24</sup>. Meanwhile, agricultural nitrogen emission (agricultural N) was much higher than agricultural phosphorus emission (agricultural P) into water (24,511 t yr<sup>-1</sup> N and 3731 t yr<sup>-1</sup> P in 2020, Supplementary Fig. S6), suggesting that nutrient inputs from agriculture may cause nitrogen enrichment and an imbalance in the N to P ratio in the water. In Hainan East coastal waters, the recorded dissolved inorganic nitrogen (DIN) concentrations reached 3 to 20 μM, and the dissolved inorganic phosphorus (DIP) reached 0.20 to 0.85 μM in 2017<sup>53</sup>, with the majority of sea area nutrient concentrations exceeding safe thresholds for coral survival (DIN < 9 μM, DIP < 0.33 μM)<sup>54,55</sup>. Chronic nitrogen enrichment can inhibit coral growth and reproduction<sup>56,57</sup>, while fueling macroalgae dominance (Figs. 1d and 3a), driving coral species diversity reduction (Supplementary Fig. S2), and influencing a persistent phase shift to algae-dominated states. Since 2012, the LCC of most reefs in Hainan East was less than 10% alongside 40% macroalgae cover (Fig. 2a), resulting in a coral-algae phase transition<sup>58</sup>. The SEM analyses show that agricultural N directly reduces LCC while enhancing the adverse effect on LCC by indirectly affecting turbidity and macroalgae (Fig. 3a), suggesting that the growing agricultural nutrient input is another major threat to local coral reefs. The degradation of Hainan East reefs reflects synergistic “top-down” (overfishing) and “bottom-up” (eutrophication from agricultural N) mechanisms. Depleted coral reef fish populations (Fig. 1e) disrupt algae grazed levels, while excess nutrients override coral resilience thresholds<sup>59,60</sup>. This dual degradation pathway—reduced top-down control and enhanced bottom-up enrichment—potentially leads to hysteresis in reef recovery, as macroalgae dominance suppresses coral recruitment and alters biogeochemical cycling.

Interestingly, SEM analyses show that the human population (POP) had a positive effect on LCC in Hainan East by indirectly affecting macroalgae (Fig. 3a). POP dynamics and migration patterns critically influence coastal ecosystem management through socioeconomic pathways<sup>22</sup>. 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 and Supplementary Fig. S5c). The urbanization process in Hainan East was primarily driven by large-scale internal migration of rural-to-urban population (Supplementary Fig. S5c),

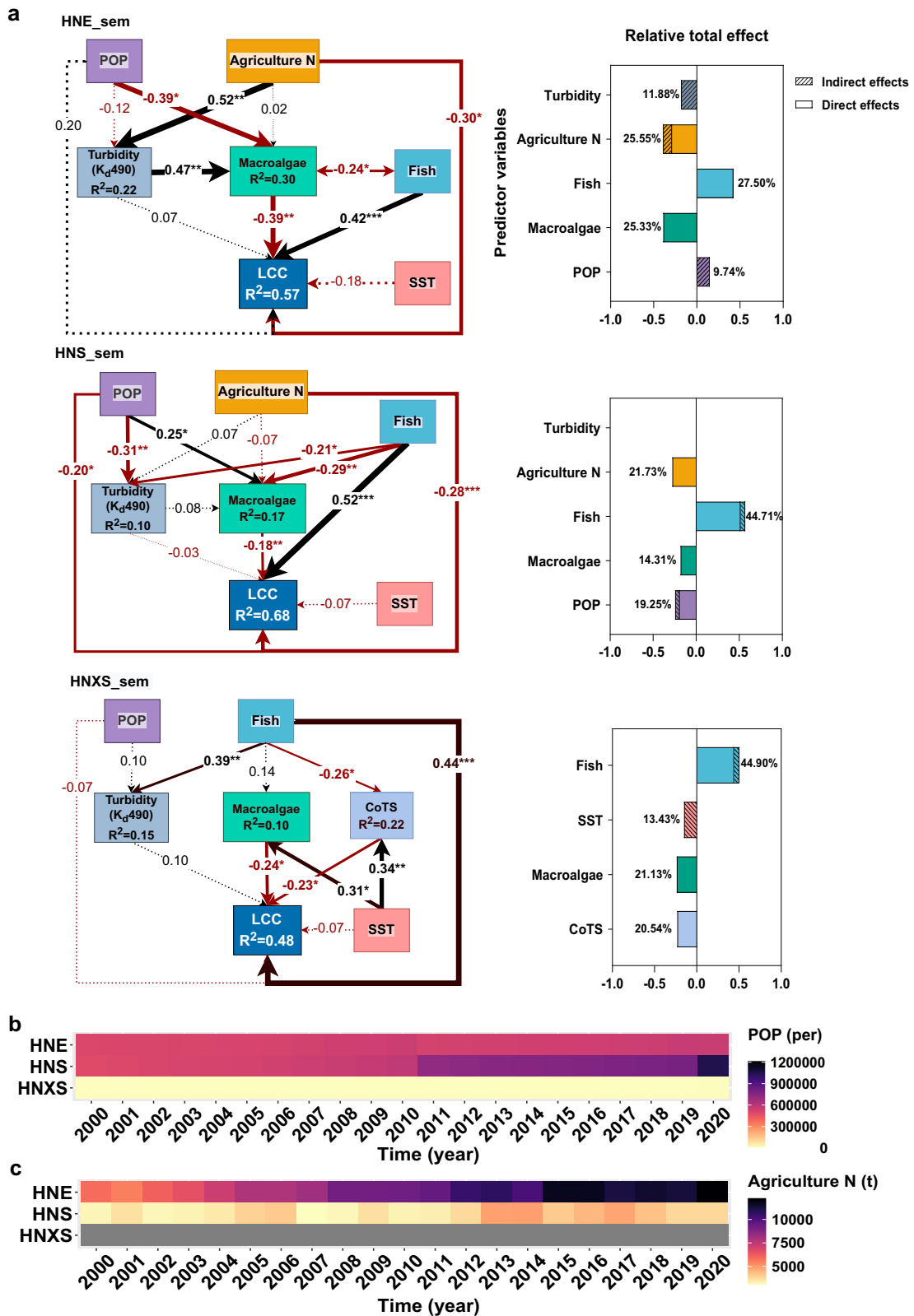


**Fig. 2 | Effects of ecological factors on live coral coverage.** **a** Relationship between ecological factors and live coral coverage in different subregions from panel model analysis. **b** The annual accumulation of typhoon exposure degree (Typhoon). **c** The annual mean  $K_4490$  (Turbidity) from remote sensing monitoring. **d** The mean sea surface temperature (SST) from remote sensing monitoring; **e** the annual maximum degree heating weeks ( $DHW_{max}$ ), indicating the intensity and time since past extreme thermal stress. **a** The dependent variables are the live coral coverage in Hainan East (HNE), Hainan South (HNS), and Hainan Xisha (HNXS), respectively. Sample sizes are 49, 106, and 64, respectively. CoTS denotes crown-

of-thorns starfish. Effect sizes are individual fixed effects fitting regression coefficients (median values) with 95% credible intervals (CIs; thin lines) and 80% CIs (thicker lines). The gray lines indicate an overlap with zero and a less credible trend (effect = 0). Positive effects (the 80% credible interval greater than zero) indicate that the probability of establishment increases with increasing values of predictive variables (blue), while the negative effects (the 80% credible interval less than zero) indicate the converse (red). For more statistical results, see Supplementary Data 3. **b–e** The yellow to purple colors indicate low to high values of data gradient, with gray denoting missing data.

which distances human activity centers from coastal reefs<sup>10</sup> 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 in controlling pollution, as environmental infrastructure expansion keeps pace with gradual population growth. Some environmental policies implemented since 2010, such as Beautiful Countryside and Sanitary City, have further improved localized environment governance<sup>61</sup>. However, these benefits are offset by



legacy nutrient accumulation and non-point agricultural pollution, underscoring the priority for targeted management of mariculture effluents and agricultural non-point source pollution<sup>59,60,62</sup>.

**Overfishing and urban sprawl induce coral mortality**

Our findings establish that rapid urban expansion and tourism development constitute primary anthropogenic drivers of coral reef

degradation in Hainan South. They act through two key pathways: water quality deterioration from inadequate wastewater management, and habitat destruction through coastal construction. The urbanization rate in Hainan South escalated dramatically from 26% in the 1980s to 70% by 2020, accompanied by an urban population surge of ~640,000 compared to a modest rural decline (<70,000) (Fig. 3b and Supplementary Fig. S5c). Driven by large-scale external migration, this

**Fig. 3 | Structural equation model (SEM) of three subregions performed to explore the direct and indirect effects of environmental variables on live coral coverage.** **a** SEM for Hainan East (HNE), Hainan South (HNS), and Hainan Xisha (HNXS). **b** Resident Population (POP) change from 2000 to 2020. **c** The change of agricultural nitrogen (N) emissions to the water from 2000 to 2020. **a** LCC denotes live coral coverage. Fish denotes the level of reef fish density. CoTS denotes crown-of-thorns starfish. Macroalgae denotes the degree of eutrophication of the water, while the diffuse attenuation coefficient of light at the 490 nm wavelength ( $K_d490$ ) denotes the turbidity of the water. SST denotes the mean sea surface temperature each year. Resident Population (POP) denotes local urban development gravity—an indicator of nearby human settlements potential influences on coral reefs (e.g., land use), while the agriculture N denotes total agriculture nitrogen emissions per year to the water in native city. **a** This SEM is determined through model comparison and

fits the data well (HNE:  $p = 0.74$ ,  $n = 49$ ; HNS:  $p = 0.45$ ,  $n = 106$ ; HNXS:  $p = 0.44$ ,  $n = 64$ ). All path coefficients were estimated using generalized linear models with two-tailed statistical tests. Boxes represent measured variables, highlighted with distinct colors, while arrows represent relationships among variables. Black and red arrows denote positive and negative effects, respectively. Dashed and solid lines denote 95% credible intervals overlapping with zero or not, respectively. Standardized path coefficients are given for each path, the width of which is scaled by the magnitude of the standardized path coefficient. The conditional  $R^2$  for each endogenous variable is reported in the corresponding boxes. The direct, indirect, and relative total effects are shown in the right part of this figure. For more statistical results, see Supplementary Data 4. **b–c** The yellow to purple colors indicate low to high values of data gradient, with gray denoting missing data.

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 (Supplementary Fig. S5d). The SEM analysis reveals that POP exerts a direct adverse impact on LCC in Hainan South and indirectly influences LCC through macroalgae increase (Fig. 3a), derived by cumulative impacts of increased sewage discharge (Supplementary Fig. S5d), coastal engineering<sup>63</sup> and sediment input, etc.<sup>64</sup>. The sharp decline in Hainan South reefs from 2007 to 2010 was due to a substantial reduction in LCC on certain reefs that were subjected to high turbidity pressure (e.g., sediment accumulation rates of  $36.0 \text{ mg cm}^{-2} \text{ d}^{-1}$  in Xiaodonghai reef)<sup>65</sup>. Our results also suggest that turbidity had a significant negative impact on the LCC in Hainan South reefs (Fig. 2a). Tourism exacerbates these pressures, with tourist numbers increasing 11.5-fold (2–23 million) between 2000 and 2019 (Supplementary Fig. S5b). Considering the influence of the large population from tourism, our results indicate tourism increases POP's negative impact on LCC by 4.46% compared to without considering tourism, exceeding agricultural N effects (Supplementary Fig. S4 and Fig. 3a). Coastal engineering activities, such as building construction and land reclamation, further degrade coastal ecosystems through eutrophication and sedimentation<sup>66,67</sup>.

While agricultural nutrient emissions demonstrate direct negative effects on LCC in Hainan South, their impacts remain comparatively limited (Fig. 3a). Total agricultural N and P emissions to water in Hainan South only increased by 0.16- and 0.6-fold, respectively, from 2000 to 2020 (Supplementary Fig. S6), with  $3835 \text{ t yr}^{-1}$  agricultural N and  $420 \text{ t yr}^{-1}$  agricultural P (Supplementary Fig. S6). Nutrient concentrations in Hainan South coastal waters (DIN:  $-3\text{--}10 \mu\text{M}$ ; DIP:  $-0.03\text{--}0.28 \mu\text{M}$ ) were typically at the threshold boundary<sup>68</sup>, where moderate levels of nutrients were detrimental to coral growth but reversible with reduced nutrient inputs<sup>45,69</sup>. Indeed, localized macroalgae increases occurred during 2010–2012 in Hainan South<sup>70</sup> before regional coverage declined and stabilized at  $-5.67\%$  (Fig. 1d) following reductions in terrestrial pollution<sup>71</sup>. This variability reflects the complex interplay of factors, with macroalgae mediating the negative effect of POP on LCC but not that of agricultural nitrogen in Hainan South reefs (Fig. 3a). The ecological changes observed here align with a reef degradation model involving top-down, side-in, and bottom-up (eutrophication and other pollution) factors. Collectively, these results highlight that the primary drivers of coral reef degradation in Hainan South are human activities associated with overfishing, urban expansion, and tourism development.

### Overfishing and CoTS outbreaks induce coral mortality

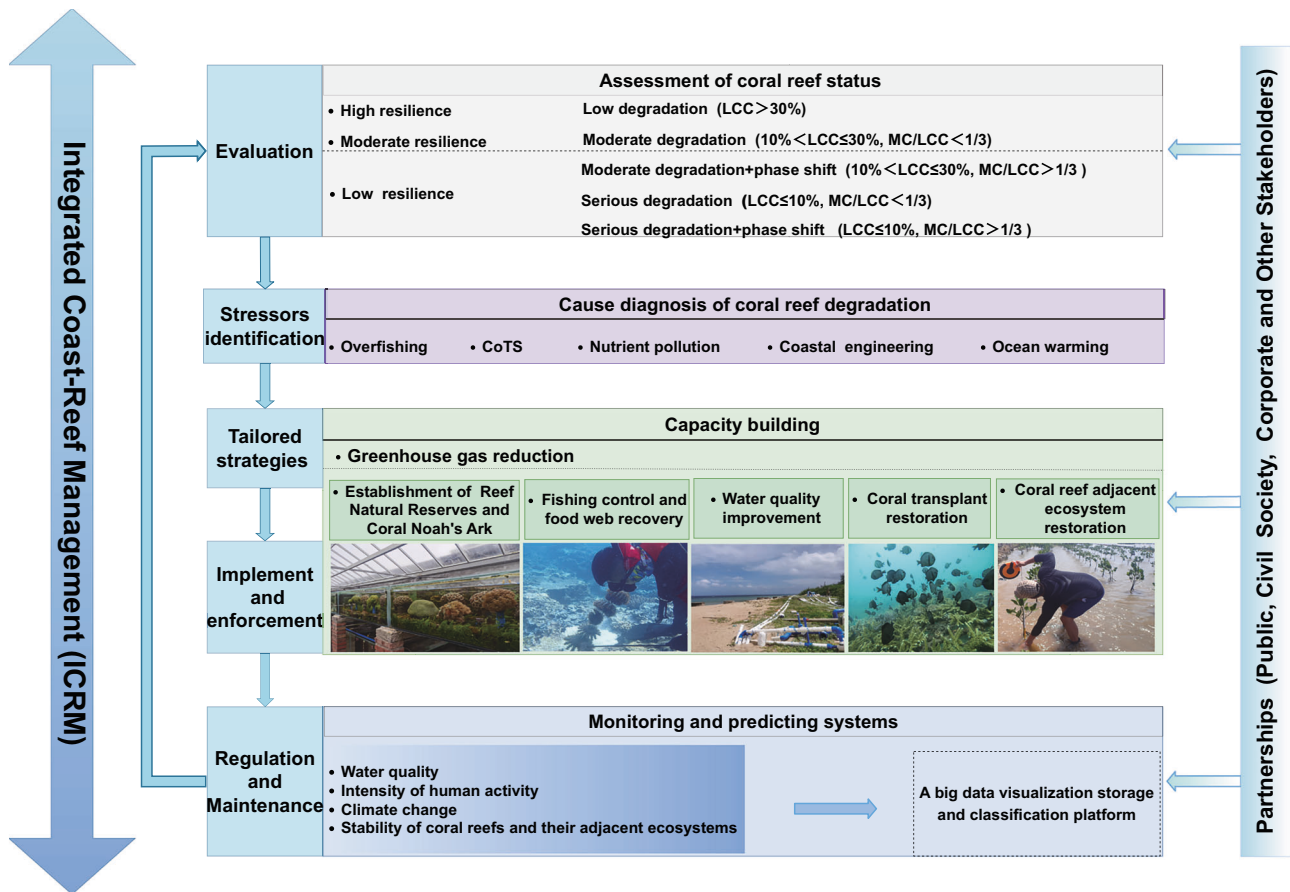
The CoTS outbreaks during 2005–2009 in Hainan Xisha (Fig. 1f) represent the second most significant stressor driving live coral cover (LCC) decline, as evidenced by the panel analysis ( $-0.25$ ,  $p = 3.1\text{e-}10$ , Fig. 2a and Supplementary Data 3) and SEM (Fig. 3a). Temporal alignment between CoTS population surges (Fig. 1c, f) and coral mass mortality events (Fig. 1c) strongly indicates CoTS outbreaks as direct

triggers of reef degradation<sup>72,73</sup>. Notably, the trajectory of dramatic reduction in reef fish density preceded and paralleled LCC loss in Hainan Xisha (Fig. 1b, e), implicating trophic cascade effects. The population of CoTS is typically regulated by predator guilds (e.g., *Charonia tritonis*, *Abudefduf curacao*, and *Chaetodon falcula*) and competitors<sup>74</sup>, whose depletion through overfishing permits CoTS outbreaks<sup>75</sup>. Despite theoretical expectations of macroalgae dominance post-disturbance, Hainan Xisha reefs showed only transient, localized macroalgae increases ( $<5\%$  mean regional coverage; Figs. 1d and 2a). This constrained response reflects favorable water quality characterized by low nutrient levels and high transparency, likely due to minimal land-based pollution in remote reefs. The panel analysis of Hainan Xisha shows that macroalgae has a negative but relatively small impact on LCC (Fig. 2a), contrasting with stronger mediation effects observed in the food chain (Fig. 3a). The Hainan Xisha degradation trajectory aligns with combined top-down (overfishing) and side-in (perturbations leading to direct coral mortality) mechanisms, where CoTS-induced coral mortality initiates ecosystem reorganization rather than classic bottom-up nutrient-driven transition<sup>28</sup>. These findings underscore that Hainan Xisha reef conservation requires dual priorities, including (1) implementation of ecosystem-based fisheries management to restore trophic balance, and (2) development of adaptive strategies for CoTS outbreak prediction and containment.

### Integrated Coast-Reef Management strategies tailored to protect local coral reefs

Existing coral reef management in the South China Sea and globally remains fragmented, lacking the multi-scale systematic approaches required to address escalating anthropogenic and climate pressures. Based on empirical results, we propose an ICRM framework (Fig. 4) that enables local actions in a systematic way to improve reef resilience under climate change. This ICRM framework provides tailored paths to local coral reef governance (Supplementary Fig. S9 and Data 5), supporting the fulfillment of United Nations Sustainable Development Goals (SDG 14) and Decade of Ocean Science priorities. The ICRM consists of five key steps (Fig. 4), including (1) Quantitative evaluation, (2) Stressors identification, (3) Tailored strategies, (4) Implementation and enforcement, as well as (5) Regulation and maintenance. This adaptive framework allows decadal-scale adjustments to shifting environmental pressures and restoration efficacy, enabling dynamic reprioritization of interventions. We further define reef-specific assessment metrics and implementation pathways for each step (Fig. 4 and see the Supplementary Note 1 for a detailed description), integrating ecological thresholds with socioeconomic drivers.

Application of the ICRM framework reveals spatial heterogeneity in reef resilience across the study regions (Fig. 4). 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. Similarly vulnerable Hainan East reefs (mean LCC  $10\text{--}30\%$ , MC/LCC  $>1/3$ ) face dual stressors of intensive fishing and



**Fig. 4 | Integrated Coast-Reef Management (ICRM) framework.** The five key elements of ICRM are in the coral restoration management process for long-term management. LCC denotes live hard coral coverage. MC marcoalgae coverage, MC/

LCC the ratio between marcoalgae coverage and live hard coral coverage, CoTS crown-of-thorns starfish.

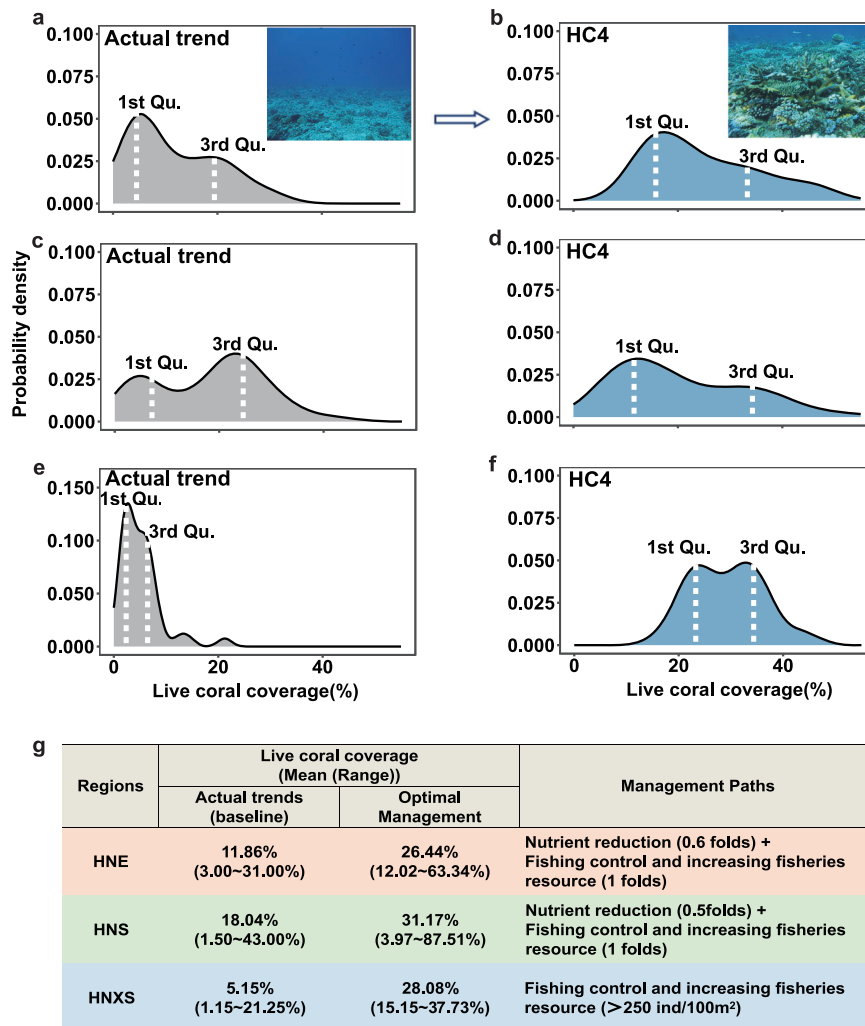
nutrient loading from adjacent agricultural runoff. While Hainan South reefs show moderate resilience (mean LCC 10–30%, MC/LCC <1/3 in most areas), their recovery capacity remains constrained by chronic urbanization pressures. Our SEM-NUFER integration provides a comprehensive perspective on system dynamics, revealing distinct stressor hierarchies, namely, fish resource depletion and nitrogen enrichment from agricultural development on the regional scale, and urbanization-driven sedimentation and sewage impacts at the local scale. This multi-model approach confirms artificial restoration necessity for low-moderate resilience reefs, given limited natural recovery capacity.

We investigated the potential impact of combinations of key drivers on the projected LCC (Fig. 5), aiming to optimize LCC levels above the minimum threshold of 10% required for carbonate production on reefs<sup>22</sup>, particularly under global warming. Drawing upon the ICRM framework, we employ a comprehensive range of methodologies to safeguard and rehabilitate local coral reefs (Supplementary Data 5). Additionally, we devise tailored strategies for mitigating the depletion of fishery resources through fish seed release initiatives, as well as implementing eco-friendly agricultural practices to minimize nutrient discharge into water bodies (see “Methods”). Specifically, we generate management scenarios to assess the impact of varying reef fish density (representing sea-based management) and nutrient pollution (representing land-based management) on the probability of falling into low, moderate, or high LCC categories.

Our findings show that the implementation of an ICRM approach can yield a favorable synergistic outcome for coral reefs (Fig. 5). When land or sea management strategies are implemented separately in the three subregions, they only result in improvements either in low-LCC

or high-LCC coral reefs (Supplementary Data 6). However, the simultaneous implementation of integrated land-sea management scenarios leads to a significant increase in LCC within the Hainan East subregion, with the minimum LCC surpassing 10% and a two to four times rise in LCC observed (Fig. 5a, b). The results of scenario analysis for Hainan South exhibit similar trends to those observed for Hainan East but with relatively modest improvement (Fig. 5c, d). In Hainan Xisha, a higher density of coral fish (e.g., over 250 ind/100 m<sup>2</sup>) would lead to a significant increase in LCC, surpassing 10% in low-LCC coral reefs (Fig. 5e, f). The sustainable development and restoration of fishery resources are the top priority in promoting local coral reef restoration in the South China Sea. Recovery of fishery resources requires additional management efforts<sup>76</sup> to the improvement of fisheries resilience, for example, through breeding and reproducing sufficient type of local fish to enhance ecosystem food webs, implementing no-take zones (including coral reefs), restoring habitat and the expanding marine protected areas (MPAs)<sup>77</sup> in the key areas of the South China Sea (Supplementary Fig. S9 and Data 5). Transboundary cooperation and similar policy implementation through Regional Seas Programs (e.g., Partnerships in Environmental Management for the Seas of East Asia, PEMSEA) among South China Sea regions/countries could be more helpful in amplifying conservation outcomes<sup>78</sup>.

Our findings suggest that the restoration pathways for both bottom-up and top-down forces may not be mutually exclusive, but rather complementary, thereby contributing to the emergence of advantageous patterns. Notably, land-based management has clear effects on low-LCC coastal coral reefs in Hainan East and Hainan South. The primary focus for managing land-based activities should be on coral reefs with low and moderate resilience. This includes



**Fig. 5 | Scenario analysis of local reef management based on the Integrated Coast-Reef Management framework.** **a, b** Actual state and best hypothetical cases for Hainan East (HNE). **c, d** Actual state and best hypothetical cases for Hainan South (HNS). **e, f** Actual state and best hypothetical cases for Hainan Xisha (HNXS). **g** These cases that represent an integrated, optimal management scenario for each region, combining the most effective interventions identified in our models to keep live coral coverage above 10% in most reefs—a threshold required for carbonate production on reefs<sup>22</sup>. **a–f** The live coral coverage in the different hypothetical cases HC1, HC2, HC3, and HC4 for the period 2011–2020. There are low, moderate (more

than the 1st Quarter and less than the 3rd Quarter percentile), and high live coral cover categories. The description of the hypothetical cases is in “Methods.” The gray shades reflect the probability density of actual live coral cover in each sub-region since 2010, while the blue parts reflect the probability density of adjusted live coral coverage by reducing nutrient (agricultural nitrogen) emissions into water, increasing fisheries resources, and hunting the crown-of-thorns starfish. **g** Different colors represent different subregions; the orange, green, and blue indicate HNE, HNS, and HNXS, respectively.

implementing green agricultural practices (e.g., precision fertilization, aquaculture industry transformation, and wetland buffers) to reduce nutrient runoff into water, as well as restoring reef habitats of Hainan East and Hainan South (Supplementary Fig. S9 and Data 5). In terms of habitat restoration, Wuzhizhou Island in Sanya, Hainan, China, is a typical restoration case, where coral reef habitats responded favorably to the implementation of effective marine management, such as the marine ranch construction<sup>79</sup>. The island’s coastal and marine biodiversity has been significantly improved, with an 18% increase in coral cover during 2017–2020 (82.9% increase contribution from transplanted corals) and an increasing occurrence of large marine organisms such as giant wild grouper, whale sharks, and tropical spotted dolphins. A recent study showed that in 2019, there was more coral cover in some regions, including the East Asia Seas, than there was in 1983 (United Nations Environment Programme). Such optimistic outcomes provide great encouragement for continued efforts in reef ecological restoration and conservation. Meanwhile, there is still a long way to go to explore the sustainable development in urban expansion

and tourism, with particular emphasis on recycling techniques that are eco-friendly in coastal engineering and wastewater treatment, aiming at minimizing land-based pollution into reef waters<sup>80,81</sup>. Notably, our scenario modeling reveals threshold effects in management outcomes. The nonlinear response of LCC to fish density (particularly in Hainan Xisha) suggests minimum biomass requirements for functional recovery, aligning with trophic cascade theories. Similarly, the disproportionate benefits of integrated land-sea management highlight the compounding impacts of concurrent stressors—a critical consideration for reef systems facing climate change pressures.

By integrating ecological, socioeconomic, and geospatial methodologies, we offer a paradigm shift in coral reef management—from global-scale diagnostics to region-specific solutions. We document coral reef degradation patterns in the northern South China Sea resulting from the interaction of top-down processes and bottom-up processes and/or side-in processes, with long-term and time-lagged effects. Using the systemic land-to-sea approach, we identify that local human activities, particularly agricultural nitrogen runoff, urban

expansion, and overfishing, are the primary drivers of reef degradation, leading to a 40% loss of LCC over two decades. Our ICRM framework provides tailored solutions by coupling land-based interventions, such as precision fertilization and wetland buffers, with marine conservation measures, such as sustainable fishing quotas and CoTS control. These strategies synergistically enhance LCC by 2- to 4-fold under a global warming scenario, enabling LCC to reach the lowest thresholds required for reef carbonate production. The findings can be immediately applied to the South China Sea to prevent ecosystem collapse and broader tropical reef regions facing similar anthropogenic pressures (e.g., Coral Triangle). Future studies that integrate broader-scale and fine-scale data are recommended.

## Methods

### Study area and historical context

Hainan Province in China, located at the north of the South China Sea, possesses around 38,000 km<sup>2</sup> of coral reefs supporting over 400 coral species<sup>49</sup>. The latitudinal range of the study region is approximately 16°N–20°N (Fig. 1a), including Hainan East (HNE, Wenchang and Qionghai city located at 19° North Latitude (NL) in this study, representing higher macroalgae and higher turbidity stress), Hainan South (HNS, Sanya city located at 18°NL, representing lower macroalgae, high turbidity, and heat stress), and Hainan Xisha (HNXS, Sansha city located at 17°NL, representing lower macroalgae and higher heat stress) (Supplementary Fig. S1). Historically, anthropogenic stressors in the Hainan reefs, including coral mining, overfishing, dredging, coastal development, and pollution, have affected coral communities for over half a century (Supplementary Fig. S3).

Local government and communities in Hainan have implemented various measures to protect and restore coral reefs (Fig. 4), including legislative protection (Supplementary Table S1), establishment of MPAs, coastal water quality improvement, and coral restoration, etc. (Supplementary Fig. S9). In the past five decades, for example, corals and coral reef protection have been an integral component of China's legal framework, encompassing laws, regulations, rules, and plans dedicated to marine ecological protection and species conservation (Supplementary Table S1). Meanwhile, a number of MPAs have been established in China since the late 1980s, including 11 nature reserves with coral and coral reefs as the main targets of protection<sup>50</sup>, covering about 262 million hectares. Restoration of degraded reefs by coral transplantation in Hainan Province's MPAs, such as Wuzhizhou Island in Sanya, Xisha Islands, and Nansha Islands, extended over 200,000 m<sup>2</sup><sup>79</sup>. Moreover, Wanning city on Hainan Island has built a land-based species protection base for reef corals and giant clams (Supplementary Fig. S9). The summer fishing ban policy in the South China Sea was established in China in 1999; however, its implementation was only strictly enforced since 2015.

### Coral reef data

Based on field survey data from the 1990s to 2020, we compiled the data to create a dataset (Supplementary Data 1) and the figures (Fig. 1 and Supplementary Fig. S1). The dataset integrated our field survey data (2002–2020) with the findings from previous studies (1990s–2001). We aggregate the LCC data by calculating the mean LCC per survey site/year, then the mean LCC per reef/year, and finally the mean LCC region/year (response variable). 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). Data from the annual monitoring survey were then binned into long-term successive and discrete types, with discrete data excluded from quantitative driver analysis. For each reef, a coral reef survey (comprehensive survey monitoring) or a simple random sample survey (sampling monitoring) is conducted annually, with at least three sites per reef for simple random sample

surveys. At each site, community substrate type was recorded by video along each  $\geq 50$  m transect line, and the linear point intercept (LPI) method was used to calculate the percentage LCC. Each coral taxon was categorized into life-history “types” based on previous studies<sup>22</sup>. Four life-history types (Supplementary Fig. S2) based on published species traits are: fast-growing competitive (e.g., *Acropora*); slow-growing and long-lived massive stress-tolerant (e.g., *Platygyra*); subdominant generalist (e.g., *Echinopora*); and fast-growing brooding weedy taxa (e.g., *Pavona*). The field work was supported by local institutes and funding from relevant governmental departments of China (see the Supplementary Methods for detailed description), following the principle of minimal impacts on the marine environment. No corals and other marine animals were collected or captured during the field research activities.

Coral species richness, coral reef fish density, MC, coral recruit (<5 cm diameter), and CoTS abundance were calculated from field surveys for the LPI. Dead coral coverage and MC (including all fleshy upright macroalgae but excluding upright calcareous algae such as *Halimeda* spp.) were collected with the LPI. A full description of coral community data collection and rationale can be found in the Supplementary Methods.

To evaluate the relative influence of climate, social, and environmental drivers (Supplementary Data 2) on total LCC, we identified a suite of covariates at reef, location, and region scales (Supplementary Fig. S1 and Table S2). These covariates 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), MC, typhoon exposure, temperature (SST<sub>warm</sub>, mean SST in warm months (May to October each year)), turbidity (K<sub>d490</sub>), 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). The dynamic assessment of agricultural N was high-resolution, quantifying city-scale terrestrial nutrient losses in food systems (crop and livestock production, aquaculture, and human consumption) to water through localized NUFER models. A full description of covariates, data sources, and rationale can be found in the Supplementary Methods.

### Data analysis

All environmental variables underwent preliminary analysis, including Pearson correlation 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  $> 5$ . 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 can be accurately and reliably estimated. A final set of 13 covariates and 2 dependent variables were included in the statistical models, whereby all pairwise correlations were  $< 0.7$ , and VIFs are  $< 5$ , indicating that multicollinearity was not a serious concern. All environmental variables were screened for collinearity and temporal coverage scale (at least 5 consecutive years of monitoring data); only those that passed both tests entered the panel regressions and SEM analyses.

Independent sample t-test was adopted to compare data at a significance level of  $p < 0.05$  (Supplementary Fig. S10 and Data 7). After comprehensive analysis, three environmental factors were selected, including SST, typhoon exposure, and turbidity (Supplementary Fig. S1 and Table S2).

Statistical analysis was carried out using the statistical package SPSS 17.0 for Windows (SPSS Inc., Chicago, IL, United States). Descriptive statistics are expressed as mean  $\pm$  standard deviation. Statistical significance is accepted at \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

**Panel model analysis.** Panel data modeling examines entity- (or individual) specific and/or time effects in order to isolate unobserved heterogeneity. Entity-specific and/or time effects are either fixed effects (FE) or random effects (RE). Fixed effect models examine the variability of the model's intercept across individual reefs or time periods. Random effect models investigate differences in the model's error variance components across individual reefs or time periods<sup>82</sup>. A long-term survey allows us to estimate the relationship between LCC and potential biotic and abiotic factors, such as temperature and MC, while controlling for compounding factors such as year and location using panel model analysis. The strategy is to first examine the probability of the panel data in hand through an ordinary least squares model. The unobserved heterogeneities are investigated using fixed effect models to determine entity-specific and time effects. The panel model compiles data on both temporal and spatial scales, which can reduce the impact of time-invariant omitted variables and improve the effectiveness of estimates. The model is fitted using the *geeglm* “*geepack*” package in R<sup>83</sup>, which has a syntax similar to *glm* and returns an object similar to a *glm* object. An important feature of *geeglm* is that an ANOVA method exists for these models (Supplementary Data 3).

$$Y_{it} = \gamma Y_{it-1} + \sum_k \beta_k X_{kit} + \mu_i + \varepsilon_{it} \quad (1)$$

where subscript *it* denotes different individuals (=reefs) *i* in time *t*, *i* = 1, ...*N*; *Y* is the dependent variable (=LCC) in the different individuals (=reefs) *i* at time *t*. *X<sub>k</sub>* is the explanatory variables affecting LCC in the model, such as fish, macroalgae, SST, and so on (Supplementary Data 4). *β<sub>k</sub>* is the estimated coefficient, *γ* is the spatial autoregressive coefficient, *μ* is the intercept, and *ε* is the error term. The detailed description of the panel model is in the Supplementary Methods.

**Structural equation model analysis.** To evaluate the direct and indirect effects of socioeconomic stressors such as agricultural N losses on LCC and assess the influence of ecological factors (SST, turbidity), we conducted piecewise SEM<sup>84,85</sup> using the R packages “*piecewiseSEM*”<sup>86</sup>. Piecewise SEM can integrate a set of component models including random effects, allowing for non-Gaussian error distributions, and is thus appropriate for our data structure. Specifically, we incorporate the POP and agricultural N losses in the subregion model, then each subregion is analyzed separately to account for sampling non-independence. Multicollinearity in each component model is checked according to the VIF. Model fits are evaluated using Fisher's *C* statistic based upon Shipley's d-sep test<sup>87</sup>, and model selection is performed using the Akaike information criterion (AIC) statistic for the d-sep test<sup>88</sup>. Standardized path coefficients for the linear mixed component models and the *R*<sup>2</sup> for the endogenous variables are calculated directly using the *piecewiseSEM* package. For the generalized linear mixed component model, we extend the method used by piecewise SEM for the generalized linear model and calculate the standardized path coefficients manually by including the standard variance of random effects. Our initial model was established based on a priori knowledge (Supplementary 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 calculate the direct, indirect, and relative total effects on establishment success (Supplementary Data 4).

We also develop another SEM (Supplementary Fig. S4) to evaluate the effect of T\_POP on LCC after incorporating tourism by taking the number of tourists per year after converting to the equivalent resident population. With the rapid development of tourism after 2010 in Hainan South, the influence brought by the large number of people from tourism cannot be ignored (23 million in

2019, Fig. S5b). 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<sup>89,90</sup>. The number of overnight tourists traveling each year was 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 represents the total resident population (T\_POP), including overnight tourists visits converted into resident equivalent per year, which denotes local urban development gravity—an indicator of the potential influences of nearby human settlements on coral reefs (e.g., water quality and land use changes).

### Hypothetical cases for the past and alternative scenarios

Based on the ICRM framework, we estimated LCC from land-sea management scenarios in the typical subregions under different hypothetical cases for 2011–2020 using the SEM. 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<sup>22</sup> (Supplementary Data 6). All hypothetical cases were built on actual trends, but differed with respect to reducing nutrient (agricultural nitrogen) emissions into water, increasing fisheries resources, and removal of the CoTS.

#### 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) emissions 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 nutrients discharged to waters, and aquaculture subsystems were projected to decrease 90% of agricultural nutrient discharge. For Hainan South, 50% of nutrients discharged to waters could be reduced through agricultural green development. For Hainan Xisha, there were 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 was projected to increase reef fish density by one-fold, where coral fish density was higher (e.g., 50 ind/100m<sup>2</sup>) 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 were 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 remained low. For Hainan East and Hainan South, there were no CoTS outbreaks, so CoTS removal measures were 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, ICRM scenarios have been implemented. For Hainan Xisha, the improvement of fishery resources through building no-take marine

reserves and enforcing the Summer Fishing Ban was projected to increase reef fish density to 250–350 ind/100 m<sup>2</sup>.

All analyses are performed in the R language for statistical computing version 4.02 (R Core Team, 2020) with associated packages *nlme* and *car*.

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

### Data availability

All data generated or analyzed during this study are included in this published article and its Supplementary Data files: Supplementary Data 1 for coral reef data and Supplementary Data 2 for socioeconomic data. The environmental remote sensing data were obtained from NASA's Earth Observing System Data and Information System (EOS-DIS) MODIS-Aqua satellite database (<https://oceansdata.sci.gsfc.nasa.gov>), and the NOAA Coral Reef Watch which conducts global monitoring of heat stress based on satellite SST data ([https://www.star.nesdis.noaa.gov/pub/sod/mecb/crw/data/5km/v3.1\\_op/nc/v1.0/monthly/](https://www.star.nesdis.noaa.gov/pub/sod/mecb/crw/data/5km/v3.1_op/nc/v1.0/monthly/)). Typhoon impact data were obtained from the China Meteorological Administration tropical cyclone database (<http://typhoon.zjwater.gov.cn/>). The socioeconomic data from 2000 to 2020 were obtained from the Hainan Statistical Yearbook. The fishing hours data for northern SCS were obtained from Global Fishing Watch (GFW) (<https://globalfishingwatch.org>).

### References

- Morrison, T. H. et al. Save reefs to rescue all ecosystems. *Nature* **573**, 333–336 (2019).
- Hughes, T. P. et al. Coral reefs in the Anthropocene. *Nature* **546**, 82–90 (2017).
- Eddy, T. D. et al. Global decline in capacity of coral reefs to provide ecosystem services. *One Earth* **4**, 1278–1285 (2021).
- Graham, N. A. J. et al. Extinction vulnerability of coral reef fishes. *Ecol. Lett.* **14**, 341–348 (2011).
- Graham, N. A. J. et al. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* **518**, 94–97 (2015).
- Beck, M. W. et al. The global flood protection savings provided by coral reefs. *Nat. Commun.* **9**, 2186 (2018).
- Birkeland, C. *Coral reefs in the Anthropocene* (Springer, 2015).
- Obura, D. et al. Vulnerability to collapse of coral reef ecosystems in the Western Indian Ocean. *Nat. Sustain.* **5**, 104–113 (2022).
- Forster, J. et al. Evidence of a common understanding of proximate and distal drivers of reef health. *Mar. Policy* **84**, 263–272 (2017).
- Cinner, J. E. et al. Bright spots among the world's coral reefs. *Nature* **535**, 416–419 (2016).
- Carriger, J. F. et al. Assessing coral reef condition indicators for local and global stressors using bayesian networks. *Integr. Environ. Assess. Manag.* **17**, 165–187 (2021).
- Lin, B. et al. Coral reefs and coastal tourism in Hawaii. *Nat. Sustain.* **6**, 254–258 (2023).
- Ellis, J. I. et al. Multiple stressor effects on coral reef ecosystems. *Glob. Change Biol.* **25**, 4131–4146 (2019).
- Hughes, D. J. et al. Coral reef survival under accelerating ocean deoxygenation. *Nat. Clim. Change* **10**, 296–307 (2020).
- Hughes, T. P. et al. Ecological memory modifies the cumulative impact of recurrent climate extremes. *Nat. Clim. Change* **9**, 40–43 (2019).
- Guan, Y. et al. Vulnerability of global coral reef habitat suitability to ocean warming, acidification and eutrophication. *Glob. Change Biol.* **26**, 5646–5660 (2020).
- Gilby, B. L. et al. Optimising land-sea management for inshore coral reefs. *PLoS ONE* **11**, e164934 (2016).
- Kroon, F. J. et al. Towards protecting the Great Barrier Reef from land-based pollution. *Glob. Change Biol.* **22**, 1985–2002 (2016).
- Wolff, N. H. et al. Vulnerability of the Great Barrier Reef to climate change and local pressures. *Glob. Change Biol.* **24**, 1978–1991 (2018).
- Gove, J. M. et al. Coral reefs benefit from reduced land-sea impacts under ocean warming. *Nature* **621**, 536–542 (2023).
- McManus, L. C. et al. Extreme temperature events will drive coral decline in the Coral Triangle. *Glob. Change Biol.* **26**, 2120–2133 (2020).
- Darling, E. S. et al. Social-environmental drivers inform strategic management of coral reefs in the Anthropocene. *Nat. Ecol. Evol.* **3**, 1341–1350 (2019).
- Bai, Z. et al. Nitrogen, phosphorus, and potassium flows through the manure management chain in China. *Environ. Sci. Technol.* **50**, 13409–13418 (2016).
- Jiao, Y. et al. Nitrogen budgets for freshwater aquaculture and mariculture in a large tropical island – A case study for Hainan Island 1998–2018. *Mar. Environ. Res.* **177**, 105642 (2022).
- Lefcheck, J. S. et al. Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. *Proc. Natl. Acad. Sci. USA* **115**, 3658–3662 (2018).
- Guiden, P. W. et al. Effects of management outweigh effects of plant diversity on restored animal communities in tallgrass prairies. *Proc. Natl. Acad. Sci. USA* **118**, e2015421118 (2021).
- Souter, D. et al. *Status of Coral Reefs of the World: 2020* (UNEP, 2020).
- Precht, W. et al. *Non-random Timing of Ecological Shifts on Caribbean Coral Reefs Suggests Regional Causes of Change* (Cold Spring Harbor Laboratory Press, 2019).
- Dai, X. J. et al. Research advances on coral reef fish biodiversity and conservation. *Chin. J. Ecol.* **40**, 2996–3006 (2021). (in Chinese).
- Hughes, T. P., Huang, H. & Young, M. A. L. The wicked problem of China's disappearing coral reefs. *Conserv. Biol.* **27**, 261–269 (2013).
- Hu, W. et al. High vulnerability and a big conservation gap: mapping the vulnerability of coastal scleractinian corals in South China. *Sci. Total Environ.* **847**, 157363 (2022).
- Yao, Y. & Wang, C. Variations in summer marine heatwaves in the South China Sea. *Geophys. Res. Oceans* **126**, e2021JC017792 (2021).
- Cybulski, J. D. et al. Coral reef diversity losses in China's Greater Bay Area were driven by regional stressors. *Sci. Adv.* **6**, eabb1046 (2020).
- Watt-Pringle, R. et al. Suppressed recovery of functionally important branching *Acropora* drives coral community composition changes following mass bleaching in Indonesia. *Coral Reefs* **41**, 1337–1350 (2022).
- Huang, W. et al. Genetic diversity and large-scale connectivity of the scleractinian coral *Porites lutea* in the South China Sea. *Coral Reefs* **37**, 1259–1271 (2018).
- Jiang, L. et al. ENSO Variability during the medieval climate anomaly as recorded by *Porites* corals from the northern South China Sea. *Paleoceanogr. Paleoclimat.* **36**, e2020PA004173 (2021).
- Abesamis, M. R. R., Ang, J. L., Robles, R. C. & Licuanan, W. Y. Recovery of coral cover on inshore fringing reefs following mass coral bleaching in the Philippines. *Coral Reefs* **42**, 99–104 (2023).
- Lyu, Y. et al. The mass coral bleaching event of inshore corals from South China Sea witnessed in 2020: insight into the causes, process and consequence. *Coral Reefs* **41**, 1351–1364 (2022).
- Walker, A. S., Kratochwill, C. A. & van Woesik, R. Past disturbances and local conditions influence the recovery rates of coral reefs. *Glob. Change Biol.* **30**, e17112 (2024).
- Yu, K. F. Coral reefs in the South China Sea: their response to and records on past environmental changes. *Sci. China Earth Sci.* **42**, 1160–1172 (2012). (in Chinese).

41. Frölicher, T. L. et al. Marine heatwaves under global warming. *Nature* **560**, 360–364 (2018).
42. Lyu, Y. et al. Evaluation of the ecological status of shallow-water coral reefs in China using a novel method and identification of environmental factors for coral decline. *Mar. Pollut. Bull.* **201**, 116227 (2024).
43. Hock, K. et al. Split spawning increases robustness of coral larval supply and inter-reef connectivity. *Nat. Commun.* **10**, 3463 (2019).
44. Johnson, J. V. et al. *Mangrove Forests Mitigate Coral Bleaching Under Thermal Stress from Climate Change* (Cold Spring Harbor Laboratory, 2021).
45. Zaneveld, J. R. et al. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nat. Commun.* **7**, 11833 (2016).
46. Li, Y. C. et al. Damages of coral reef ecosystem by the giant clam excavation—a case study on North of Xisha Islands. *J. Appl. Oceanogr.* **34**, 518–524 (2015). (in Chinese).
47. Mcmanus, J. W. et al. Effects of some destructive fishing methods on coral cover and potential rates of recovery. *Environ. Manag.* **21**, 69–78 (1997).
48. Tun, K. et al. A regional review on the 2010 coral bleaching event in Southeast Asia. In *Status of Coral Reefs in East Asian Seas Region 2010* (eds Kimura, T., Yeemin, T., Cabanban, A., Doan, C. V. & He, S. H.) 9–27 (Ministry of the Environment, 2011).
49. Allgeier, J. E. et al. Fishing down nutrients on coral reefs. *Nat. Commun.* **7**, 12461 (2016).
50. Loh, T. et al. Indirect effects of overfishing on Caribbean reefs: sponges overgrow reef-building corals. *PeerJ* **3**, e901 (2015).
51. Zhang, P. et al. Spatiotemporal variation, composition of DIN and its contribution to eutrophication in coastal waters adjacent to Hainan Island, China. *Reg. Stud. Mar. Sci.* **37**, 101332 (2020).
52. Duprey, N. N. et al. Reefs of tomorrow: eutrophication reduces coral biodiversity in an urbanized seascape. *Glob. Change Biol.* **22**, 3550–3565 (2016).
53. Guo, J. et al. Nutrient distribution in coral reef degraded areas within Sanya Bay, South China Sea. *J. Coast. Res.* **33**, 1148 (2017).
54. Donovan, M. K. et al. Nitrogen pollution interacts with heat stress to increase coral bleaching across the seascape. *Proc. Natl. Acad. Sci. USA* **117**, 5351–5357 (2020).
55. Zhao, H. et al. Impacts of nitrogen pollution on corals in the context of global climate change and potential strategies to conserve coral reefs. *Sci. Total Environ.* **774**, 145017 (2021).
56. Bruno, J. F. et al. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* **90**, 1478–1484 (2009).
57. Herbeck, L. S. et al. Effluent, nutrient and organic matter export from shrimp and fish ponds causing eutrophication in coastal and back-reef waters of NE Hainan, tropical China. *Cont. Shelf Res.* **57**, 92–104 (2013).
58. Li, X. et al. Linking benthic community structure to terrestrial runoff and upwelling in the coral reefs of northeastern Hainan Island. *Estuar. Coast. Shelf Sci.* **156**, 92–102 (2015).
59. Cheng, G. et al. Rural human settlement environment improvement: process, status and China's sample. *Environ. Develop. Sustain.* **27**, 17805–17832 (2025).
60. Herbeck, L. S. & Unger, D. Pond aquaculture effluents traced along back-reef waters by standard water quality parameters,  $\delta^{15}\text{N}$  in suspended matter and phytoplankton bioassays. *Mar. Ecol. Prog. Ser.* **478**, 71–86 (2013).
61. Xia, J. et al. Exploring the spatial–temporal analysis of coastline changes using place name information on Hainan Island, China. *ISPRS Int. J. Geo-Inf.* **10**, 609 (2021).
62. Shi, Q. et al. Human activities and impacts on coral reef at the Luhuitou fringing reef, Sanya. *Trop. Geogr.* **30**, 486–490 (2010). (in Chinese).
63. Li, X. et al. Coral community changes in response to a high sedimentation event: a case study in southern Hainan Island. *Chin. Sci. Bull.* **58**, 1028–1037 (2013).
64. 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 Res. Part II Top. Stud. Oceanogr.* **96**, 88–96 (2013).
65. Zhang, J. et al. Land–sea interactions at the east coast of Hainan Island, South China Sea: A synthesis. *Cont. Shelf Res.* **57**, 132–142 (2013).
66. Zhang, P. et al. Spatiotemporal river flux and composition of nutrients affecting adjacent coastal water quality in Hainan Island, China. *J. Hydrol.* **591**, 125293 (2020).
67. Houk, P. et al. Nutrient thresholds to protect water quality and coral reefs. *Mar. Pollut. Bull.* **159**, 111451 (2020).
68. Titlyanov, E. A. & Titlyanova, T. V. Changes in the species composition of benthic macroalgal communities of the upper subtidal zone on a coral reef in Sanya Bay (Hainan Island, China) during 2009–2012. *Russ. J. Mar. Biol.* **39**, 413–419 (2013).
69. Li, X. et al. Benthic flora of coral reefs in heavily nutrient-polluted areas of Sanya Bay (Hainan Island, China) and its changes recorded after removing the source of pollution. *Russ. J. Mar. Biol.* **47**, 105–113 (2021).
70. Wu, Z. J. et al. The analysis on the reason of hermatypic coral degradation in Xisha. *Acta Oceanol. Sin.* **33**, 140–146 (2011). (in Chinese).
71. Li, Y. C. et al. Analysis on the outbreak period and cause of *Acanthaster planci* in Xisha Islands in recent 15 years. *Chin. Sci. Bull.* **64**, 3478–3484 (2019). (in Chinese).
72. Yao, Q. C. et al. A review of research on crown-of-thorns starfish and their ecological effects on coral reefs. *Acta Ecol. Sin.* **42**, 7517–7528 (2022). (in Chinese).
73. Kroon, F. J. et al. Fish predators control outbreaks of Crown-of-Thorns Starfish. *Nat. Commun.* **12**, 6986 (2021).
74. Li, Y. et al. Social–ecological vulnerability and risk of China's marine capture fisheries to climate change. *Proc. Natl. Acad. Sci. USA* **121**, e2313773120 (2024).
75. Benedetti-Cecchi, L. et al. Marine protected areas promote stability of reef fish communities under climate warming. *Nat. Commun.* **15**, 1822 (2024).
76. Sun, Y. et al. Joint protection of a crucial reef ecosystem. *Science* **377**, 1163 (2022).
77. Yu, C. et al. Managing nitrogen to restore water quality in China. *Nature* **567**, 516–520 (2019).
78. Donovan, M. K. et al. Local conditions magnify coral loss after marine heatwaves. *Science* **372**, 977–980 (2021).
79. Kimura, T. et al. Status and Trends of East Asian Coral Reefs: 1983–2019. *Global Coral Reef Monitoring Network, East Asia Region*. Japan Wildlife Research Center and Ministry of the Environment, Tokyo. (2022).
80. Huang, H. et al. *Status of Coral Reefs in China (2010–2019)* (Ocean Press, 2021) (in Chinese).
81. Huang, H. et al. Coral reef habitat and resources restoration in tropical island marine ranching. *Sci. Technol. Develop.* **16**, 225–230 (2020). (in Chinese).
82. Ben-Romdhane, H. et al. Studying coral reef patterns in UAE waters using panel data analysis and multinomial logit and probit models. *Ecol. Indic.* **112**, 106050 (2020).
83. Højsgaard, S. et al. The R package geepack for generalized estimating equations. *J. Stat. Softw.* **15**, 1–11 (2006).
84. 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).
85. Shipley, B. Confirmatory path analysis in a generalized multilevel context. *Ecology* **90**, 363–368 (2009).

86. Lefcheck, J. S. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2016).
87. Bill, S. A new inferential test for path models based on directed acyclic graphs. *Struct. Equ. Model.* **7**, 206–218 (2000).
88. Shipley, B. The AIC model selection method applied to path analytic models compared using a *d*-separation test. *Ecology* **94**, 560–564 (2013).
89. Chen, H. & Li, L. A study on the differentiation of tourists' stay length in Hainan. *J. Guizhou Univ. Commer.* **1**, 53–57 (2012). (in Chinese).
90. Shan, X. et al. Mitigation of greenhouse gas emissions and nitrogen losses caused by migration and tourism in China's tropical island cities. *J. Environ. Manag.* **393**, 127054 (2025).

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## Author contributions

H.Z., H.X., Y.L., and L.M.C. conceptualized the study and are the senior authors. H.Z., H.X., T.L., X.S., and Z.L. were involved in methodology, including how to use data and inputs. Y.L., H.X., X.L., J.L., S.C., Z.W., X.S., and Z.L. contributed to coral reef monitoring data and human activity investigation. H.X., B.W., C.Y., and S.K. were involved in visualization and conceptual development. H.X., T.L., and H.Z. wrote the original draft,

with input from L.M., Z.B., X.L., D.H., L.M.C., T.J., S.Z., D.Y., Q.L., W.K., Y.H., X.D., and H.H. All authors contributed to review and editing.

## Competing interests

The authors declare no competing interests.

## Additional information

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