

Synergistic effects of interconnectivity among coral reefs, seagrass beds, and mangroves under climate change

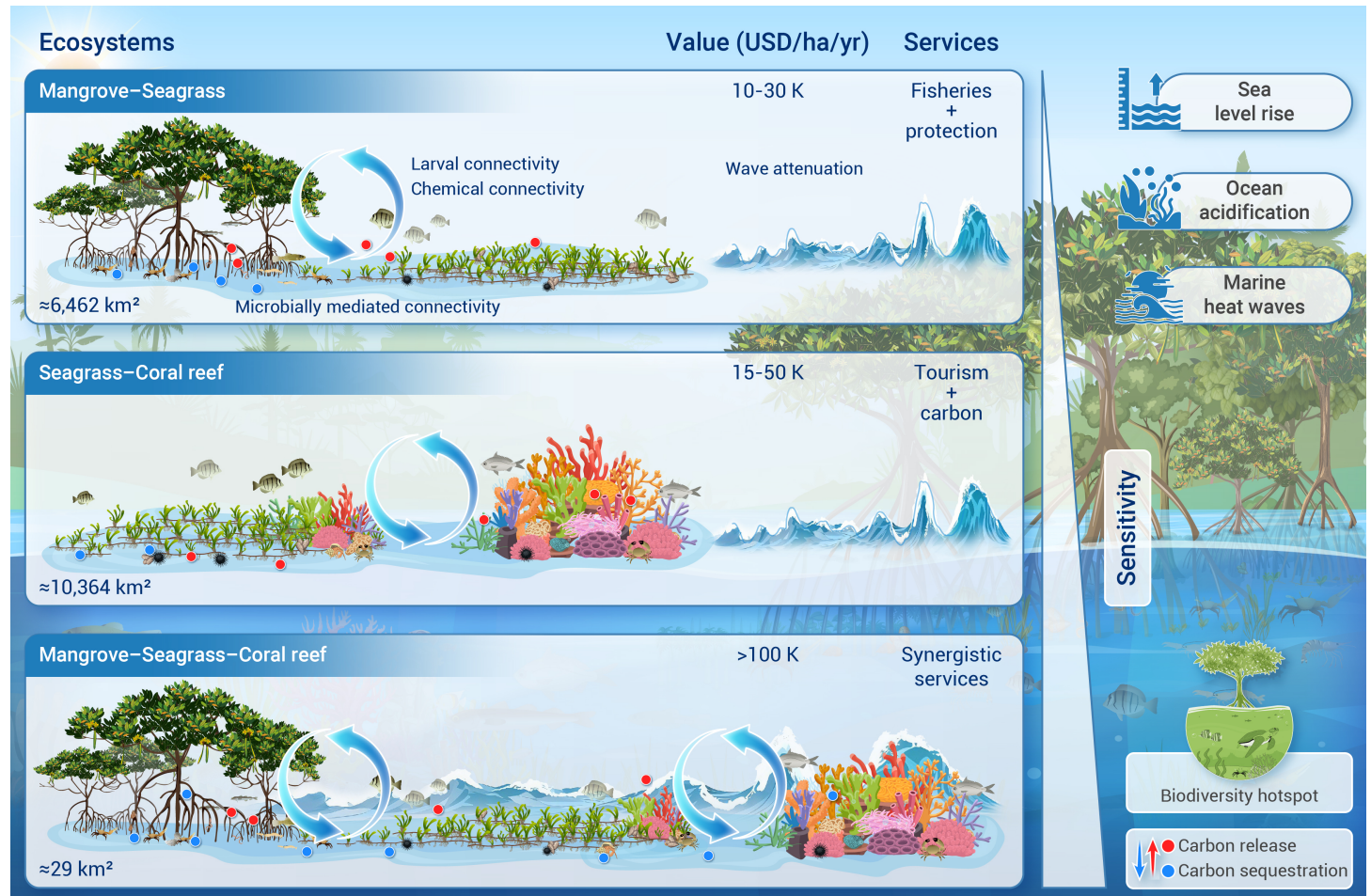
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Received: October 18, 2024; Accepted: December 4, 2025; Published Online: January 4, 2026; <https://doi.org/10.59717/j.xinn-geo.2026.100189>

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GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Coral, seagrass, and mangrove ecosystems are interconnected and enhance coastal resilience.
- This connectivity supports biodiversity, protects shorelines, and helps fight against climate change.
- These vital ecosystems are threatened by climate change and human activities.
- We propose integrated management to conserve them as a single, connected unit.

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Received: October 18, 2024; Accepted: December 4, 2025; Published Online: January 4, 2026; <https://doi.org/10.59717/j.xinn-geo.2026.100189>

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Citation: Mao W., Geng X., Huai Z., et al. (2026). Synergistic effects of interconnectivity among coral reefs, seagrass beds, and mangroves under climate change. *The Innovation Geoscience* 4:100189.

The interconnectivity among coral reefs, seagrass ecosystems, and mangroves (CSM) forms a critical ecological continuum that sustains biodiversity, enhances resilience to environmental stressors, and supports coastal communities. This study reviews the synergistic interactions between these interconnected ecosystems under climate change, highlighting their importance in carbon sequestration, ocean acidification, shoreline protection, and biodiversity conservation. We examine how cross-ecosystem fluxes of organisms, nutrients, and energy enhance resistance and recovery to climate stressors, including ocean acidification, sea level rise, and marine heat waves. Despite their critical role, these ecosystems face significant vulnerability, and their continued decline poses a direct threat to coastal resilience and ecosystem services. The review emphasizes the necessity of maintaining habitat connectivity, which is integral to species survival and ecosystem function. A comprehensive conservation strategy is proposed, advocating for a polycentric governance model to address the complexities of CSM interactions, incorporating multiple stakeholders to promote sustainable management and policy coordination. Critical research gaps are identified, particularly in understanding the underappreciated role of seagrasses in marine conservation and the poorly understood spillover effects between CSM ecosystems. The study calls for a unified, evidence-based approach to coastal management that enhances the resilience of CSM ecosystems, mitigates climate impacts, and ensures the long-term sustainability of these invaluable systems for future generations.

INTRODUCTION

Coral reefs, seagrass meadows, and mangroves (CSM) are three essential coastal ecosystems in tropical regions around the world (Figure 1).

Coral reefs are underwater structures formed by colonies of coral polyps typically found in shallow waters. Seagrasses are aquatic plants that also inhabit shallow coastal areas in the tropics, and can cover large extensions of soft sediments forming dense seagrass meadows. The third interlinked ecosystem crucial for marine biodiversity and coastal protection in tropical regions is mangrove forests, a group of salt-tolerant trees or shrubs that thrive in the intertidal.¹ Intertidal mangroves and seagrass meadows promote biodiversity, serving as nurseries for aquatic flora and fauna, stabilizing sediments and reducing the rate of erosion in coastlines.^{1,2} They also purify water (thus reducing the pH in the water that can lead to coral smothering and bleaching protection) while aiding in wave reductions and carbon sequestration.³⁻⁵ Mangroves play an additional pivotal role in biogeochemical connectivity and trophic foundation by exporting essential nutrients, such as organic carbon and nitrogen, that fuel microbial activity and primary production in adjacent ecosystems.^{6,7} The microbially mediated cycling of nutrients between mangroves and seagrass meadows represents a fascinating example of ecosystem connectivity in tropical and subtropical coastal zones.

Coral reefs also offer shelter to both algal bio-mats and seagrass beds from larger waves, and are fundamental to maintaining marine biodiversity by providing habitat to a large array of species.⁸ CSM ecosystems are

not only productive and vital ecosystems but are also among the most endangered globally.⁹ Despite their proximity and ecological interdependence, conservation efforts have often treated these ecosystems in isolation, as single independent units. However, when preserved together these ecosystems offer synergistic benefits that surpass those provided independently,^{10,11} mutually enhancing resilience against environmental disturbances.¹² CSM ecosystems occupy vast coastal areas in the Eastern Asia-Pacific region while appear less common in order bioregions (Table 1).

However, areal coverage estimates in some regions, particularly the tropical Indo-Pacific region, are suspected to be underestimated due to limited historical monitoring efforts. Still, there is general consensus that CSM ecosystem have experienced significant losses over the last century at an increasing rate of deterioration.¹³⁻¹⁵ In a comprehensive synthesis of data obtained from 175 studies spanning between 1880 and 2016, Dunic et al.¹⁶ reported the net loss of 5,602 km² (19.2%) of the areal extent of seagrasses meadows historically recorded. They observed the fastest decline during the early 20th century, with a more comprehensive data analysis revealing significant declining trends in the Tropical Atlantic and Mediterranean between the 1940s and the 1980s. Among the major causes for this decline are those associated to anthropogenic activities; i.e. direct impacts associated to coastal development and dredging, as well as indirect impacts resulting from the degradation of the water quality. Meanwhile, the devastating impacts associated to global climate change are predicted to become more recurrent (Figure 2).

Similarly to seagrasses, the extent of coral reef cover has shrunken drastically during the last century and nowadays their coverage is limited to one half of the historical records.^{13,17,18} The reduction in the capacity of coral reefs to provide ecosystem services has been attributed to a variety of natural fluctuations and anthropogenic stressors. Global warming and acidification of the ocean have facilitated coral mass bleaching and disease outbreaks in the past while deterioration of the local environmental conditions associated to eutrophication and overfishing have magnified the negative impacts. Guannel et al.¹⁰ simulated how small changes in global and local stressors would affect the suitability of coral reefs. They suggested that 61% of the reefs worldwide would be affected by the simultaneous effects of local and global stressors and only 6 % of them will remain unaffected by any of them.

Mangroves have also suffered severe consequences due to deforestation and habitat degradation, and a number of species are catalogued under serious risk of extinction.¹⁹⁻²¹ Deforestation for exploitation of timber and urban expansion appeared as major cause of mangroves were lost during the 20th century.^{14,22,23} During the 1980s and 1990s, at least 35 % of the mangrove forests were lost.²³ The reduction in deforestation rates during the 2000s have alleviated the pace of mangrove loss which is primarily caused by commodity-based land-use changes, particularly the conversion to shrimp aquaculture and rice agriculture.²⁴

Growing concerns and compromises to the preservation of healthy ocean ecosystems are reflected in the international agendas to attain the UN Sustainable Development Goals. The number and extension of protected areas have recently expanded steadily, and currently, over 43% of coral reefs,

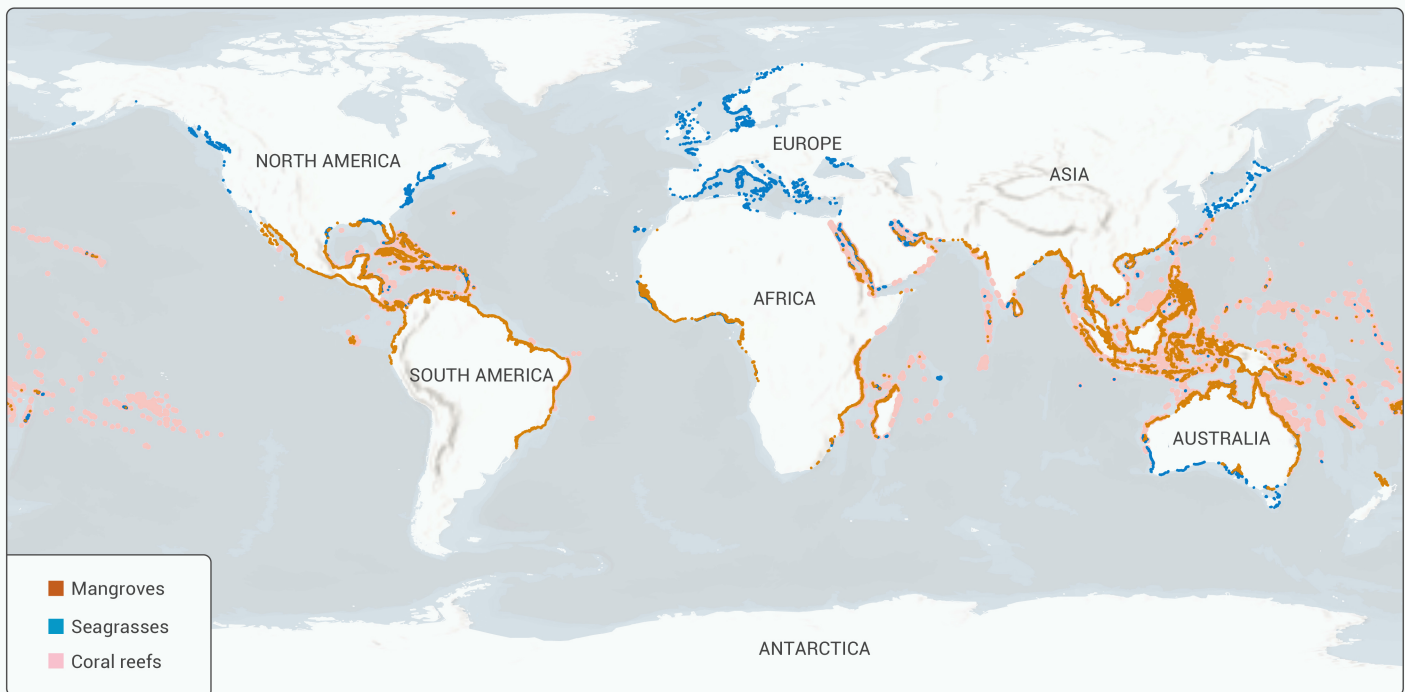


Figure 1. Global overlap of CSM. Coral reef to seagrass: 10,364 km², coral reef to mangrove: 5,011 km², seagrass to mangrove: 6,462 km², three ecosystem overlap: 29 km²
Overlap of one ecosystem over another.¹⁻³

Table 1. Global coverage of CSM in km² by regions.

Region	Mangrove	Seagrass	Coral Reef	References
East Asia-Pacific	31,823	264,528	159,425	19,110,111
North America	43,010	4614	27,623	19,70,110
Latin America & the Caribbean	40,522	4101	27,623	19,70,110
Africa	27,956	68,503	15,179	19,110,112
Europe	insignificance	869	2,000	110,113,114
Oceania	17,221	83,013	41,802	19,110
Middle East	198	7,000	13,605	19,110,115

26% of seagrass meadows and 40% of mangroves are protected.²⁵ Yet, the benefits of seagrass protection has been often overlooked and not covered by management plans, hence the significantly smaller degree of protection. Coral reefs also present some major protection gaps. While tourism values of protection appear clearly recognized, the relevance of coral reefs for coastal protection appears not fully understood in most coral reef nations.²⁶ Major regional gaps of data represent another major obstacle to conducting comparative studies that can provide insights into the status and services provided by CSM, as well as the synergetic interactions among interconnected ecosystems. This information is crucial to delineate comprehensive management strategies to guaranty healthy protection and preservation of these ecosystems.

We reviewed the currently available literature covering the interconnectedness among the CSM ecosystems, focusing exclusively on tropical regions where these ecosystems dominate as primary producers. Ecosystems such as salt marshes and kelp forests were excluded due to geographic emphasis. The review explores patterns of habitat degradation or disturbances driven by anthropogenic and climate change. Lastly, we discuss barriers to joint land-sea management and outline future research work to support the connected conservation of these three ecosystems. This interdependence underscores the necessity of a holistic approach to management for conservation and protection. By viewing CSM as a single, integrated unit rather than isolated ecosystems, need more effective safeguards that benefit the CSM contin-

uum. This holistic perspective is fundamental to the polycentric governance model proposed later, as it addresses the complex interactions in CSM ecosystems.

Predicting species distributions and developing conservation strategies requires understanding ecosystem connectivity and how it interacts with climate change.²⁷ Conservation efforts should be directed to create well-connected networks among CSM ecosystems, restore habitats, and aid colonization. Examining ecological, socio-economic, and policy dimensions can also help ensure resilience and sustainability. This comparative analysis helps identify areas needing more attention in the CSM ecosystem connectivity area.

ECONOMIC DIMENSION OF CSM ECOSYSTEMS

As a collective, CSM ecosystems support the Gross National Product (GNP) of many countries. While assigning a monetary value to CSM is challenging due to variations in per capita incomes, legal frameworks, and inflation rates across territories, several studies have attempted to estimate their value in economic terms. Despite these complexities, an increasing number of studies have provided robust economic assessments of their role in sustaining livelihoods and supporting national economies. The most frequently recognized services include coastal protection and erosion control,²⁸⁻³¹ fisheries,^{28,29,32,33} tourism and recreation,^{29,31} and carbon sequestration are important ecosystem services provided by CSM identified for their

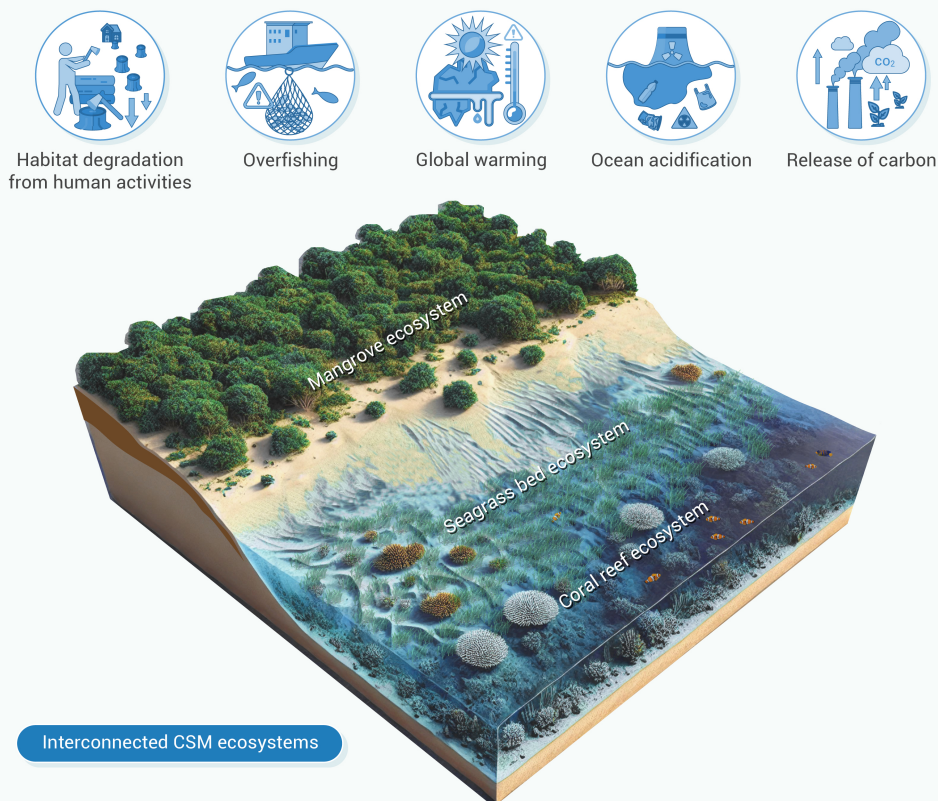


Figure 2. Climate change and anthropogenic pressure impacts affecting CSM Connectivity.

presented in Table 3.

Mangroves sequester carbon at an estimated rate of $\sim 6\text{--}8\text{ tCO}_2\text{e/ha/yr}$,⁴⁵ while seagrasses $\sim 1.5\text{--}4.4\text{ tCO}_2\text{e/ha/yr}$, according to NASA ARSET blue-carbon training materials from 2024. More recently, mangrove restoration credits have sold for approximately \$27.8 per tonne. Mangrove carbon credits issued by projects in Asia and Central America are currently being offered in the \$13–\$35/mtCO₂e range.⁴⁶ Why coral reefs show “not applicable”: under current accounting and crediting frameworks, coral reefs aren’t treated as long-term net CO₂ sinks (calcification/biogeochemistry issues), so they generally are not eligible for blue-carbon offsets. Although they deliver many other benefits (coastal protection, fisheries, and tourism), they do not contribute to the removal of “blue carbon” in the present day.

Blue carbon markets have grown, and credits from restoration projects are selling for more in voluntary frameworks (like the Verified Carbon Standard) co-benefits like biodiversity enhancement.⁴⁴ However, constraints like transaction costs, additionality verification, and permanence risks make it hard to scale up,

economic relevance.^{32,34–36}

Several key services provided by CSM ecosystems contribute to their economic significance, as shown in Table 2. Beyond these roles CSM provide others indispensable functions, such as water purification and nutrient cycling, filter terrestrial runoff, mitigate eutrophication, and improve offshore water quality, reducing the need for costly artificial filtration systems.³⁶ Furthermore, they serve as biodiversity reservoirs, supporting a disproportionate amount of marine life and maintaining genetic diversity that is crucial for ecosystem resilience and potential bioprospecting.³⁴ The role of mangroves and seagrasses in sediment stabilization and the facilitation of primary production forms the foundational basis of the coastal food web, without which fisheries would collapse.³⁵

The primary source of income from marine tourism worldwide is coral reefs. Mangroves generate significant value through specialized ecotourism, resource extraction, though these activities often involve significant trade-offs with other service provisions.³⁷ Their role as natural infrastructure for coastal protection, attenuating wave energy and preventing erosion, avoids billions of dollars in annual damages to coastal property and infrastructure.³⁸ This protective function is increasingly valued in the context of climate (Table 3).

Numerous studies have estimated the economic value of CSM ecosystem services based on market-based approaches (e.g., replacement costs), revealed preferences (e.g., travel costs), or stated preferences (e.g., contingent valuations).³⁸ Several studies have showed the economic value of CSM’s important ecosystem services. These values are frequently based on market-based methods. In Table 3, highlighting how each type contributes disproportionately to ecosystem stability. A key part of CSM’s economic value is its position in blue carbon markets, where carbon credits turn sequestration services into a form of currency. CSM works well as a sink because it has high productivity and anaerobic sediments.³⁹ Their remarkable efficiency in sequestering carbon is demonstrated by the fact that they cover less than 2% of the ocean area,⁴⁰ store over 30,000 TgC ($\approx 110.1\text{ GtCO}_2\text{e}$), which is comparable to the total carbon stored in terrestrial forests,^{41,42} and remove $\approx 0.862\text{--}1.652\text{ GtCO}_2\text{e yr}^{-1}$, which is five times higher per hectare than terrestrial forests making them an as key assets in climate mitigation.^{43,44} Global estimates of sequestration potential and illustrated monetary values are

therefore policy changes are needed.⁴⁷ Between 2014 and 2025, 6.96 million blue carbon credits (BCCs) were issued and 3.65 million retired, predominantly transferred from least developed and developing countries to developed nations at below-market value.⁴⁴ The economic dimensions of CSM highlight their necessity for sustainable development, necessitating improved value systems and investment in conservation.⁴⁸

CARBON CYCLING AND SEQUESTRATION ACROSS THE CSM ECOSYSTEMS

Seagrasses meadows and mangroves represent important ecosystems for carbon storage and sequestration in the ocean. Through photosynthesis, seagrasses and mangroves fix inorganic carbon dioxide (CO₂), which is then converted into organic carbon. The heterotrophic carbon components absorbed by mangroves and seagrass through photosynthesis are partially reintroduced into the sediments and hydrological carbon cycles or stored via the plant body.⁴⁹ In mangrove and seagrass ecosystems, only 25% to 50% of organic carbon originates from the net primary productivity of coastal vegetation,²⁴ while more than 50% to 75% of organic carbon is derived from allochthonous carbon pools (marine and terrestrial sources).¹⁸ A portion of the heterotrophic carbon in the detritus is exported out through hydrodynamic processes, contributing to the deep carbon burial or serving as a nutrient source for other marine ecosystems.⁵⁰ Coral reefs are not direct net absorbers of CO₂, as mangroves and seagrasses, but their close association make them indispensable to reduce carbon emissions and the impact of climate change. They contribute to carbon fixation by absorbing carbon dioxide through their symbiotic relationship with the photosynthetic algae zooxanthellae. Corals also need to incorporate carbon to build their skeletal structures of CaCO₃, while they release some carbon dioxide during the biological calcification process.^{51,52}

As interconnected CSM ecosystems, a fraction of the organic carbon exported from mangroves is taken up by seagrasses while another part contributes to the carbon storage pool deposited in the sediments, favored by their complex root systems that prevents resuspension with wave action.^{42,53,54} Coral reefs also enhance the blue carbon potential of the CSM ecosystem by buffering seagrasses against hydrodynamic forcing.⁵⁵ Some organic carbon from upstream sources enters the heterotrophic coral reef

Table 2. Economic Values of CSM Ecosystem Services.

Ecosystem Service	Ecosystem Type	Economic Value (US\$)	Scale	Reference
Tourism & Recreation	Coral Reefs	36 billion	Annual, global	26
	Mangroves	37,927 ha ⁻¹ yr ⁻¹	Per hectare, per year	116
Coastal Protection	Coral Reefs	350,000 ha ⁻¹ yr ⁻¹	Per hectare, per year	117
	Coral Reefs	9 billion	Annual, global	29
Fisheries	Coral Reefs	5.7 billion	Annual, global	118
Carbon Sequestration	All CSM (Mean)	\$US 6–42yr ⁻¹	Annual, global	47
	Seagrass (S.E. Asia)	214.6 - 249.4 million	Total for region	119

Table 3. Blue Carbon Sequestration and Valuation.

Ecosystem	Global area (Mha)	Typical sequestration (tCO ₂ e/ha/yr)	Est. annual sequestration (MtCO ₂ e/yr)	Illustrative value at \$20/t (USD/yr)	Broad value range* (USD/yr)
Mangroves	14.5	6–8	101.5 (87–116)	\$2.03B	\$0.43B–\$4.06B
Seagrass meadows	30.0	1.5–4.4	90.0 (45–132)	\$1.80B	\$0.23B–\$4.62B
Coral reefs	—	—	—	Not applicable	Not applicable

food web, thus promoting the carbon cycling within the entire coral reef ecosystem.

Seagrasses present one of the largest carbon sinks capacity per area basis, although they only cover 0.1% of the ocean floor.^{14,22} They display the largest overall cumulative sequestration potential among marine ecosystems with a mean value of 44 Mt C yr⁻¹ and a removal rate of 221 g C m⁻² yr⁻¹.¹⁷ The upper 1 m of seagrass is estimated to contain 19.9 Pg C, equal to the emissions of fossil fuels and cement production in 2014.¹⁷ Meanwhile, mangrove forests stand as the leading marine habitat for storage of carbon per unit area with a mean estimate of 738.9 Mg C ha⁻¹, totaling 6.17 Pg C of the mean global stock.⁵⁶ In conserved and protected form, blue carbon can be stored in the sediments for millennia,^{40,57} but they can shift to becoming a sources of carbon emissions when disturbed.^{58,59} Mangroves are capable of absorbing and sequestering up to four times more CO₂ from the atmosphere than rainforests.⁵¹ Yet, due to the smaller area they cover, it only represents 0.4–7% of the global carbon of terrestrial ecosystem.⁵⁶ Additionally, coral reefs contribute sinking approximately 70 to 90 megatons of carbon annually to build their CaCO₃ skeleton.⁶⁰

CSM ROLE IN OCEAN ACIDIFICATION & CLIMATE CHANGE MITIGATION

Ecologically connected ecosystems are considered more resilient to climate change, storing large amounts of carbon than individual ecosystems.⁵⁴ Indeed, the capacity of CSM for blue carbon sequestration and storage has been highlighted as a fundamental ecosystem service against climate change.^{20,61} When atmospheric CO₂ enters into contact with the ocean surface, it reacts with the water molecules producing carbonic acid and releasing hydrogen. As the amount of atmospheric CO₂ increases, the natural exchange rate of carbon deviate from equilibrium and the absorption of excess atmospheric CO₂ leads to ocean acidification (OA).

The photosynthetic potential of seagrass meadows contributes to enhance carbonate chemistry dynamics and mitigate the effects of OA in marine ecosystems. By combining biological and ecological mechanisms, seagrass meadows can buffer pH and help ameliorate the adverse effects of OA.^{21,62} Mangrove forests have also proven their relevance to mitigate the effects of climate change and OA.⁴² The intricate root systems of mangroves and their ability to adapt to saline environments enable them to filter and regulate water quality and reduce acidity levels. Coral reefs are particularly vulnerable to ocean acidification. A decrease in pH levels reduces the amount of carbonate ion available in water, impairing the calcification processes of coral reefs and shell-forming organisms, hindering the potential for buffering ocean acidification and compromising the health of marine food webs and ecosystems worldwide. Mangroves and seagrass meadows have proven beneficial for reef-building corals against the adverse effects of climate change.^{63,64}

Lower bleaching rates have been observed in coral reefs shaded by mangroves compared to adjacent reef tracts, with this association providing significant mitigation against thermal stress, ocean acidification, and solar radiation.⁶³ Association with seagrass meadows have also shown favorable responses in coral reefs against ocean acidification. Besides chemical buffering, mangroves and seagrass habitats can also facilitate the recruitment of corals when ocean acidification limits the availability of hard substrate.⁶⁵ Corals grow in symbiosis with photosynthetic algae (*Zooxanthellae*) which provide the essential nutrients, but these symbionts are spelled under stress conditions, and corals loose color and start bleaching. The result can be corals becoming more heterotrophic and relying on other nutrient sources, including planktonic diazotrophs (nitrogen-fixing bacteria).⁶⁶

The importance of understanding and preserving the synergistic interactions between CSM ecosystems to enhance their resilience under the growing challenges of climate change has become evident in many tropical regions around the world.^{67–69} In the Maldives, rising sea temperatures and ocean acidification threaten coral reefs, leading to sedimentation that affects adjacent ecosystems.⁷⁰ Similarly, in the Seychelles, bleaching events such as the 1998 coral mortality incident have had cascading impacts on mangroves and seagrass beds, affecting water quality and ecosystem stability.⁷¹ In Florida, USA, rising sea levels and warming temperatures have caused seagrass diebacks, which in turn affect mangroves and coral reefs, diminishing ecosystem services and showcasing the compounded effects of climate stressors.⁷² Examples from the Caribbean Sea have also illustrated the potential of marine reserves in fostering ecosystem resilience.⁷³ Protected areas with healthy CSM ecosystems have shown greater resistance to hurricanes and climate stressors, highlighting the critical role of connectivity in mitigating environmental impacts.

In addition, rising water temperatures are causing marine heatwaves to happen more often, last longer, and be more violent. These short bursts of severe heatwaves are a direct and deadly threat to CSM ecosystems, causing coral bleaching and death events that damage the structure and function of reefs.⁷⁴ Heatwaves affect seagrass species and have less ability to photosynthesize, while mangroves may die if they reach their thermal limitations.⁷⁵ Marine heatwaves are becoming more common, and they are becoming a major cause of rapid ecological degradation. They often work with other stressors to cause collapse.

CSM BIODIVERSITY & HABITAT CONNECTIVITY DYNAMICS

Connectivity is crucial to maintaining the integrity and resilience of CSM ecosystems. Marine connectivity comprises both active migration as well as passive transportation associated with oceanographic dynamics. Connectivity between habitat patches promotes dispersal and the preservation of

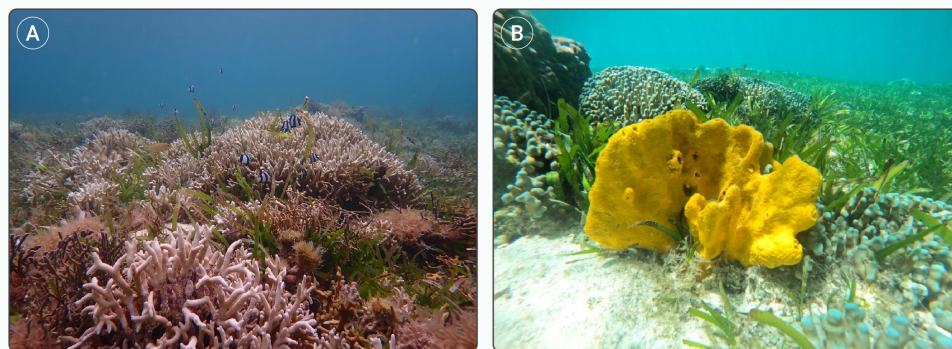


Figure 3. Symbiotic relationship of seagrass and coral reef in South China Sea, China.

genetic diversity, fundamental components to survive and thrive.⁷⁶ CSM are very productive ecosystems that support rich biodiversity and offer exceptional opportunities for feeding, reproduction and shelter within relatively small coastal areas.¹⁸ Indeed, many species take advantage of CSM connectivity to perform ontogenic habitat shifts according to their specific requirements at particular times of the year or stages along their life cycle.⁷⁷⁻⁷⁹ For many reef fish species, for example, a coral reef is often the primary habitat of adults while seagrasses and mangroves serve as nurseries and refuges during earlier life stages.⁸⁰ Approximately 20% of commercial fish species and up to 90 % of fish in mangrove areas use multiple habitats to survive.⁸¹ When coral reefs are connected to mangrove resources, the biomass of several Caribbean reef fish species have seen to double.⁸⁰ In contrast, climate-induced coral bleaching can disrupt these dynamics, reduce fish populations and impact fisheries and biodiversity, emphasizing the cascading effects of ecosystem degradation.^{82,83} In Indonesia, the destruction of mangroves for aquaculture has led to increased erosion, nutrient runoff, and sedimentation, which harm seagrass and coral reef ecosystems.⁸⁴ In the Philippines, typhoon-induced mangrove degradation increases sedimentation, leading to cascading ecosystem declines in seagrass beds and coral reefs.⁸⁵ There is increasing evidence of the potential benefits of incorporating interconnected habitat types into rehabilitation efforts to enhance fisheries management and conservation policies.⁸⁶⁻⁸⁸ Figure 3A, depict a healthier system where seagrass meadows and reef organisms live together. This improves water quality, stabilizes sediments, and provides habitat that supports more species. It shows how seagrass meadows help coral reefs stay strong and healthy in general. At other hand, Figure 3B shows a coral reef that has been damaged and has lost some of its richness. This highlights how fragile reefs can be when they don't have enough ecological support.

Abiotic vectors can also facilitate physiological and biochemical processes by the exchange of material, nutrients and energy, thus promoting dynamic trophic connectivity between these interlinked systems.⁷⁹ Microbial community and chemical pathways play also a fundamental role in ecosystem functioning and resilience by facilitating the exchange of nutrients within interconnected CSM ecosystems.^{70,89} Climate-induced changes in temperature, salinity, and oxygen availability will reshape microbial community structure and function across the CSM continuum. Ocean acidification may select for acidophilic taxa, while marine heatwaves can destabilize established microbial networks, disrupting nutrient cycling pathways critical for ecosystem resilience. Therefore, conserving CSM connectivity requires maintaining not only physical habitat linkages but also the microbial communities that sustain fundamental biogeochemical processes.

Recent predictions of the Intergovernmental Panel on Climate Change (IPCC) anticipate the rise of 0.4-0.8 m in sea level as result of ice melting, thermal expansion and change in land water store resources.⁶⁹ These changes in ocean dynamics will expose tropical marine habitats, including CSM ecosystems, to new ecological and physico-chemical challenges with far-reaching consequences for ecosystems services and human communities.⁹⁰ The consequences will be particularly notorious for low lying island states such as those where CSM ecosystems overlap. Rising of sea levels will inundate and erode shorelines forcing coastal communities to relocate millions of people. It will also alter the hydrodynamics and connectivity between CSM ecosystems and challenge the adaptive response of the marine biodiversity.⁶⁶ Following an earthquake in Solomon Islands in 2007,⁶⁶

tion was observed within a small geographical scale. It is important to note that although coral reefs benefit from moderate sea-level rise in some scenarios, increased water depths can reduce the light they require for photosynthesis,⁹² and face limitations regarding their vertical growth potential and accommodation area.⁸⁸

CSM facing threats (habitat degradation, overfishing, OA, and physical damage) are all interconnected and mutually reinforcing. The loss of these ecosystems undermines their ecological functions, such as carbon storage and habitat provision, and threatens biodiversity and the livelihoods of communities that depend on marine resources. It is difficult to prevent coastal ecosystems from being disconnected and conserved effectively due to a number of factors, including a lack of data, a lack of technological resources, and a lack of coordination among stakeholders. To overcome these barrier Table 2 show, propose solution. The degradation of CSM disrupts the ecological connectivity that is essential for maintaining the resilience of marine environments.

SYNERGISTIC THREATS TO CSM CONNECTIVITY

There is a complex synergy of anthropogenic and climate-driven threats that threaten the interconnection of coral CSM. By disrupting the connectivity, biodiversity, ecosystem services, and coastal protection are threatened.⁸⁸ These systems are increasingly vulnerable not only as a result of individual stressors, but also as a result of their compounded effects, in which each threat amplifies the impact of the next, creating a challenging conservation and protecting issue.^{89,91} Marine heatwaves cause severe physiological stress that directly breaks biological connections. Mass coral bleaching damage complex reef habitats, destroying nursery and adult grounds for fish and invertebrates. This disrupts ontogenetic migration patterns that rely on the CSM continuity. For example, during a heatwave, the loss of live coral cover declines more than 50%, which affects fisheries production.⁸² This loss of biological interconnectedness represents a rapid and severe loss of ecosystem function and services.

SLR is a dominant climate-induced threat, directly jeopardizes the geomorphic and biological processes underlying CSM connectivity. The differential responses of CSM to this issue threaten and reduce connectivity among them. Mangroves face 'coastal squeeze,' where their capacity for landward migration is impeded by human infrastructure, leading to a net loss of protective function.³² As seagrasses meadows become deeper, light will be less available, resulting in seagrass meadow die-offs and the release of huge amounts of stored carbon.⁹² While coral reefs might keep pace with moderate SLR through vertical growth, this capacity is often constrained by other stressors like poor water quality.⁴ This differential response drowning of mangroves, light limitation for seagrasses, and constrained coral growth disrupts the ontogenetic migrations of fauna and the exchange of organic materials, thereby undermining the very synergy that defines the CSM continuum.

These climate threats are exacerbated by direct anthropogenic pressures, including habitat degradation from coastal development, pollution from agricultural runoff, and overexploitation of resources, which directly sever connections and weaken ecosystem resilience.⁹³ The loss of one ecosystem amplifies vulnerabilities across others; for instance, mangrove deforestation increases sediment loads that smother adjacent seagrass and coral habitats. This interplay between global climate forces and local human impacts

Table 4. CSM connectivity, conservation, and Barriers.

①Awareness deficiency about CSM economic values of CSM ecosystems ②Limited resources, manpower and availability of modern technologies used in CSM monitoring and conservation	③Deficient and patchy data if CSM distribution and conservation ④Lack of coordination between seagrass, coral, and mangrove conservationists and sharing data connection between these groups	⑤Distance between conservationists and policymakers and government agencies ⑥Conflicts between stakeholders and local communities such as local aqua-culturists and agriculturist
PATHWAYS TO OVERCOME BARRIERS:		
Time series data collection and monitoring: ①Data collection globally and share with the scientific community: Provide funds for conservationist and monitoring communities to improve data collection about CSM connectivity and inhabiting species. Utilize satellite imaging and remote sensing, LiDAR (Light Detection and Ranging), AUVs (Autonomous Underwater Vehicles), Environmental DNA (eDNA), and GPS to gather robust data.¹²⁰⁻¹²² ②Citizen Science programs: involved local communities in data collection. It will increase awareness and residents will own the CSM habitats and will provide alternative jobs in these areas to reduce dependency on natural resources and CSM habitat use Strengthened political will: ③Empower local leaders: Engage influential community leaders in policy dialogues with government agencies and NGOs to advocate for conservation.^{123,124} ④Local stewardship: Foster pride in conservation success.¹²⁵	⑤Set and amend legal and policy frameworks to protect the ecosystem as priorities.¹²⁶⁻¹²⁸ ⑥Development measurable targets: National governments should set clear, measurable conservation targets for CSM ecosystems as part of their environmental policies.^{129,130} ⑦Development of international cooperation: Set international cooperation between countries, especially those with shared marine and coastal ecosystems, for CSM conservation.¹³¹⁻¹³³	Coordinated management strategies: ⑧Integrated management: implements the CSM ecosystems as one ecosystem due to their interconnectedness and sharing habitat for different species and resources for different life stages of diverse species within and between CSM.^{130,134,135} ⑨Collaborative platforms: set up integrated forums that unite governments, NGOs, scientists, students, industrialists, and local communities to facilitate coordination and knowledge exchange in conservation efforts.^{136,137} Sustainable financing: ⑩Dedicated resources: Support CSM ecosystem conservation and restoration through targeted financial mechanisms.^{138,139} ⑪Develop alternative livelihood options, such as eco-tourism, that alleviate human pressure on CSM ecosystems.^{130,140,141} ⑫Payment for Ecosystem Services (PES): maintain healthy CSM ecosystems through PES schemes that reward communities and landowners.¹⁴²

creates a feedback loop of degradation, making the protection of connectivity more urgent and complex.

However, the path to effective conservation is obstructed not only by these biophysical threats but also by profound systemic barriers. Implementing conservation strategies that address these synergistic threats requires overcoming persistent socio-economic and governance and logistical barriers. Effectively addressing the biophysical threats is difficult without first overcoming these implementation barriers. A synthesis of these barriers and a framework of evidence-based solutions to overcome them are presented in Table 4, providing a diagnostic roadmap for policymakers.

Underscores that the preservation of CSM connectivity is ultimately a socio-ecological challenge. It highlights that barriers such as deficient data, limited resources, lack of coordination among stakeholders, and conflicts with local livelihoods are often the primary reasons conservation efforts fail. Success, therefore, hinges on adopting integrated, polycentric governance models that promote collaboration across agencies and sectors, use advance technology for monitoring, and implement sustainable financing mechanisms like Payments for Ecosystem Services (PES) to align conservation with economic incentives. Thus, securing the future of these vital ecosystems requires a dual approach that simultaneously addresses the synergistic biophysical threats they face and the systemic socio-economic and governance barriers that prevent our ability to protect them.

CSM ECOSYSTEMS PORTFOLIO & SHIFTS IN SPECIES DISTRIBUTION

In the context of ecological conservation, genes, species, functional roles, and ecosystems can all be viewed as ecological portfolios, which play an integral part in protecting the ecosystem.⁸⁴ When one habitat faces disproportionate stress, a nearby alternative habitat can provide refuge for mobile organisms.⁸⁷ This dynamic could result in shifts in species distributions, mitigating total species loss and fostering competition between species. Multiple studies have shown that corals living on or near mangrove roots are less affected by bleaching events than corals living on exposed corals following those events.^{85,91,92}

It is anticipated that the encroachment of one ecosystem into other coastal habitats (mangrove-seagrass/coral) will occur as a result of factors such as changes in rainfall patterns, global temperature rises, and sea level rises.^{93,94} Ecological implications of this encroachment include altered nutrient storage, reduced storm damage, and impacts on habitat for large migratory birds and foraging bats.⁹⁵ Moreover, woody plants are likely to alter various ecosystem processes in herb-dominated marshes, with consequences that vary from region to region.⁹² In many cases, species range shifts have been observed to have minimal or no ecological consequences. Anthropogenic activities and climate change are causing unprecedented species loss, including CSM. Protecting a variety of coastal ecosystems, however, may mitigate the loss of species during the Anthropocene. As a result of climate change, mangroves and seagrasses continue to encroach on new areas, which highlights the broader, interconnected challenges facing coastal ecosystems, including coral reefs.

While synergistic conservation emphasizes the interconnected nature of CSM ecosystems, spillover effects where conservation actions in one ecosystem can benefit others remain an important, yet underexplored, aspect of ecosystem management. Understanding these effects is key to enhancing the efficiency of conservation strategies.

Spillover Effects Among CSM Ecosystems

The spillover effects among interconnected ecosystems, such as seagrass meadows, mangroves, and coral reefs, are essential to maintaining ecological balance and biodiversity.¹⁰ Spillover from an ecological perspective refers to the cross-boundary unidirectional movement of biomass, nutrients, energy, and organisms from a donor habitat to the adjacent recipient habitat that is affected by the organism.¹⁶

These interactions, facilitated by nutrient flows, species migrations, and biogeochemical processes, create synergistic relationships that enhance ecosystem functionality and resilience. The quantification of these fluxes is critical for moving beyond a static view of ecosystems towards a dynamic understanding of their mutualistic dependencies. The ontogenetic migration

of species represents well-substantiated form of spillover. For example, mangrove and seagrass habitats function as primary nursery grounds, providing food resources and predation refuge for juvenile stages of species. Upon reaching maturity, migrates to adjacent coral reefs, protect reef fish populations. This trophic relay represents a critical export of energy, biomass, productivity, and species richness of reef communities directly linked to proximity and connectivity to these nursery habitats.²

Apart from species movement, biogeochemical spillovers create vital metabolic linkages. Mangrove forests export substantial quantities of dissolved organic carbon (DOC) and particulate organic matter (POM), which are assimilated into the food webs of adjacent habitat.⁹⁶ Conversely, seagrass meadows can mediate the chemical environment of surrounding waters, creating spatial refugia for Conversely, seagrass meadows can mediate the chemical environment of surrounding waters, creating spatial refugia for stress-sensitive species.^{97,98}

Furthermore, physical and functional spillovers support the stability of CSM. The complex three-dimensional structure of coral reefs dissipates wave energy. This attenuation protects fragile mangrove seedlings from physical dislodgement and reduces sediment resuspension over seagrass beds, maintaining the light environment necessary for their productivity. In return, the extensive root systems of mangroves stabilize coastal sediments, reducing turbidity and preventing the smothering of coral reefs and seagrass meadows, thereby preserving their ecological functions.⁴⁵ The disruption of these spillover dynamics through habitat fragmentation or degradation breaks these vital linkages, leading to declines in productivity and resilience across the CSM continuum. Consequently, conservation and management strategies must adopt an integrated, ecosystem-based approach that facilitate these spillover effects.

To explore these spillover effects comprehensively, robust methodologies and frameworks are required. Ecological Network Analysis (ENA) provides a quantitative approach to modelling nutrient flows, energy transfers, and disturbance propagation across ecosystems.⁹⁹ By conceptualizing mangroves, seagrass, and coral reefs as nodes in an interconnected network, ENA identifies critical pathways and feedback loops that sustain ecosystem services.¹⁰⁰ Dynamic ENA models have recently been applied to coastal ecosystems, yielding insights into nutrient cycling and trophic interactions.^{101,102} Complementing ENA, Agent-Based Modelling (ABM) simulates the non-linear dynamics of species interactions, human activities, and environmental stressors across ecosystems. ABM has been used to predict cascading effects of habitat degradation, offering practical scenarios for adaptive management.^{103,104}

The integration of socio-economic dimensions through Coupled Human and Ecological Systems (CHES) frameworks provides a comprehensive understanding of how human activities, such as coastal development, influence ecosystem connectivity and functionality. CHES has been employed to assess the impacts of urban expansion on mangroves and seagrass ecosystems, highlighting strategies for harmonizing conservation objectives with economic growth.⁴⁷ Furthermore, spatial econometrics and geospatial modelling offer powerful tools to map spillover effects and spatial dependencies, enabling precise identification of conservation priorities. Recent advancements in machine learning-enhanced GIS have enhanced the capacity to model nutrient transport and species dispersal between habitats, providing actionable insights into ecosystem management.¹⁰⁵

Empirical case studies validate these theoretical frameworks and illustrate practical applications of spillover dynamics. For instance, Verweij et al.¹⁰⁶ documented how seagrass meadows contribute to coral reef fish populations, demonstrating the importance of ecosystem connectivity for sustaining fisheries. Such studies emphasize the critical need for integrative, evidence-based approaches to address the complex interactions among interconnected ecosystems.

In short, the exploration of spillover effects among mangroves, seagrass meadows, and coral reefs requires a multidisciplinary approach that combines ecological, spatial, and socio-economic methodologies. Advanced tools such as ENA, ABM, CHES, and geospatial modelling provide the necessary framework to deepen our understanding of these interactions and their implications for biodiversity and resilience. Integrating these methodologies

into conservation strategies will enable the mitigation of anthropogenic impacts, the enhancement of ecosystem connectivity, and the sustainable management of these vital habitats.

CONCLUSION

Throughout this paper, we have reviewed the ecological importance of maintaining connectivity among coral reefs, seagrass meadows, and mangroves. As the impacts of global climate change escalate, there is a growing worldwide push to expand protected areas that optimize ecosystem function, carbon sequestration, wildfires, floods, droughts and benefits for communities.¹⁰⁷ Ecosystem connectivity plays a crucial role in this endeavour, enabling the transfer of benefits across various ecoregions. Conservation efforts should not only focus on protecting individual habitats but also on ensuring the interdependence of these ecosystems to maximize biodiversity, enhance resilience, and support ecosystem services. Coastal ecosystems, known for their high connectivity, offer significant biodiversity returns from ocean conservation efforts.¹⁰⁸ Among these, CSM are particularly vulnerable land-sea ecosystems that yield substantial synergistic conservation advantages when safeguarded collectively. By identifying global locations where CSM overlap, we highlight four key conservation improvements resulting from the integrated management of these ecosystems: (1) enhanced resilience against threats by leveraging boundary habitats to buffer disturbances from land and sea, (2) fostering rich biodiversity within compact geographic areas, (3) generating habitat portfolio effects that create refuges for displaced organisms, and (4) boosting economic incentives through mutually supportive ecosystem services.

However, despite recognized importance of these dynamics, several research gaps in understanding their complexities hinder joint conservation efforts in CSM. Notably, the spatial extent of spillover effects between systems remains poorly understood. While Scavo Lord¹⁰⁹ indicate increased coral recruitment near mangroves, uncertainties persist regarding the spatial scale of connectivity influenced by factors like species ranges, local hydrodynamics, and bathymetry. The majority of research on CSM interactions predominantly examines the impact of mangroves on reefs, highlighting the need for studies that explore the reciprocal effects of reefs on mangroves, seagrasses, and associated species like fisheries. Understanding how disturbances in coral reefs affect nearby seagrasses or mangroves and vice versa, the implications of reef loss on different stages of seagrass and mangrove development, and the cascading impacts of specific degradation processes like coral bleaching on neighboring ecosystems are critical research areas.

There is a significant study gap in measuring how CSM connection affects how ecosystems respond to heatwaves. There is an urgent need to quantify the degree to which interconnected habitats offer thermal buffering and micro-refugia, assess the residual impacts of heatwaves on species migration and trophic interactions, and to predict how the degradation of one ecosystem (e.g., a bleached coral reef) modifies the susceptibility of neighbouring mangroves and seagrasses to future warming events.

Furthermore, significant research gaps exist in the fundamental ecology of CSM interactions, particularly in the understudied benefits of seagrass conservation it often overlooked as a conservation priority due to its uncharismatic nature, plays a crucial role in supporting marine ecosystems. Public awareness and scientific understanding of the benefits of seagrasses to society, coupled with their global decline, present challenges in prioritizing their conservation efforts. Addressing these gaps and enhancing monitoring tools for seagrasses are essential steps in advancing their conservation. Additionally, conflicting findings on the role of mangroves as climate refugia for corals underscore the need for further research to determine how mangrove-inhabiting corals contribute to reef health and establishment, especially in the face of environmental challenges like hurricanes.

In conclusion, the increasing urgency to expand protected areas for ecosystem function and carbon sequestration underscores the importance of ecosystem connectivity, particularly in coastal regions. Joint conservation efforts for CSM offer significant benefits but are hindered by research gaps. Future studies should focus on understanding the reciprocal impacts within CSM, addressing knowledge gaps in CSM conservation, and enhancing

monitoring tools to support effective land-sea spatial planning initiatives. Addressing these knowledge gaps necessitates the adoption of advanced scientific methodologies and integrative frameworks that encompass ecological, spatial, and socio-economic dimensions to provide actionable insights for ecosystem conservation and management. Collaborative research efforts across disciplines are crucial for providing policymakers with timely and coherent information to drive informed decisions in land-sea conservation.

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FUNDING AND ACKNOWLEDGMENTS

This research has received funding from the National Natural Science Foundation of China (42276235) and the Hainan Province Science and Technology Special Fund (ZDYF2023SHFZ172). The authors are grateful for the constructive comments provided by the editor and reviewers, which helped improve the quality of this manuscript. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

AUTHOR CONTRIBUTIONS

W.M and S.A conceptualized, designed and organized this study and wrote the paper. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

Data are available from the corresponding author upon reasonable request.