Synergistic benefits of conserving land-sea ecosystems

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ABSTRACT

Mangroves, seagrasses, and coral reefs interact in tropical regions throughout the world. These ecosystems exhibit strong synergies, as the health of each ecosystem supports the functioning of adjacent habitats. We present a global spatial analysis of mangrove, seagrass, and reef communities, identifying regions where these habitats co-occur. While only an estimated 18\% of interaction zones are covered by protected areas, boundaries between mangroves, seagrasses, and reefs represent areas of high conservation efficiency, where benefits of conservation amplify synergistically as land-sea ecosystems are jointly managed. We discuss four types of conservation efficiencies in these coastal ecosystems: (1) increased resistance to disturbance through inter-ecosystem feedbacks, (2) high biodiversity within small geographic areas, (3) habitat portfolio effects giving rise to climate refugia, and (4) synergistic ecosystem services, where building one ecosystem service inherently increases others. Given these synergistic benefits, global campaigns to expand marine and terrestrial protection should focus on the tightly connective interface between mangroves, seagrasses, and reefs, in order to more efficiently build resilience within and between these habitats.

1. Introduction

Coral reefs, mangroves, and seagrasses (CMS) coexist and interact throughout the tropics. Considerable research and management efforts have focused on conserving these ecosystems, particularly as they experience increasing damage and decline from climate change, overharvesting (deforestation, overfishing, reef dredging), and pollution. Conservation efforts often target these systems individually but additional action is urgently needed to jointly manage these ecosystems. Given the tight ecosystem connectivity between CMS, enhanced protection in one ecosystem can benefit adjacent habitats, suggesting that integrated conservation at the land-sea margin is greater than the sum of its parts (i.e., conservation in land and sea separately) (Stoms et al., 2005).

CMS inhabit a dynamic land-sea transition zone that facilitates beneficial interactions (Fig. 1). Mangroves and seagrasses serve as nurseries and shelter for reef fish (de la Torre-Castro and Rönnbäck, 2004; Jackson et al., 2015; Whitfield, 2017; Rogers and Mumby, 2019), and all three habitats participate in biogeochemical and trophic exchange facilitated by migratory coastal organisms (Parrish, 1989). In addition, mangroves and seagrasses regulate sediment discharge from the land, mitigating extreme sediment flows that may otherwise smother corals (Victor et al., 2004; De Boer, 2007; Golbuu et al., 2008). Reefs and seagrasses, in turn, can protect mangroves from wave action and drive beneficial biotic exchange with mangrove communities (Ogden, 1988). Beyond these ecological linkages, CMS may channel different types of human activity toward each other; for example, reefs can catalyze increased tourism that may alter land use and mangrove cover (Fig. 1). The interactions between CMS are thus fundamental to conserving each ecosystem.

Integrated land-sea planning remains challenging in practice. Quantifying land-sea processes often requires complex modeling in data-scarce settings, which is difficult to complete in the short timescales of coastal management plans. Terrestrial and marine spaces are usually managed by multiple government agencies that lack legal mandates or protocols to share authority (Brown et al., 2019). In
order to improve land-sea planning, prior research has pointed to the need for (1) outcome-based rather than threat-based models (e.g., estimating fish yields rather than pollution release), (2) “rules of thumb” and default values for rapid planning (Saunders et al., 2017), (3) a focus on return on investment from different protection scenarios (Klein et al., 2010; Beher et al., 2016), (4) Bayesian approaches for capturing uncertainty (Brown et al., 2017), and (5) spatial planning tools to optimize coastal ecosystem services (Arkema et al., 2014; Hamel et al., 2017; Brown et al., 2019). From a governance perspective, land-sea conservation requires a polycentric approach, integrating stakeholders across coastal and watershed zones to fill data gaps and achieve buy-in (Oleson et al., 2017).

In the following review, we summarize existing research on the connectivity between CMS. We largely exclude other coastal ecosystems, such as salt marshes and kelp forests, because we focus on tropical regions where CMS are common and vulnerable primary producers. We first present a global spatial analysis of regions where CMS coexist, and where they are protected. Next, we provide a brief discussion of trends in habitat degradation and disturbance in the Anthropocene in all three systems. We then systematically outline the interactions between these unique communities, identifying conservation efficiencies that arise from jointly protecting CMS. When these systems are protected together, they may provide synergistic benefits by (1) increasing resistance to disturbance across ecosystem boundaries, (2) supporting high biodiversity by providing heterogeneous resources for organisms at different life history stages, (3) creating portfolio effects, where alternative habitats can support displaced organisms, increasing the stability of each system, and (4) disincentivizing harmful human activity. We conclude by discussing barriers to joint land-sea management, and provide a roadmap for future research that can support the joint conservation of these three vulnerable ecosystems.

2. Spatial trends in mangrove-seagrass-reef habitats

From 2000 to 2016, about 0.13% of mangroves were lost each year due to aquaculture, urban expansion, and other human drivers (Hamilton, 2013; Hamilton and Casey, 2016; Goldberg et al., 2020). Mangrove deforestation has decreased since the 1980s, when mangroves were cleared at a rate of 0.99% per year, with recent improvements attributed to both increased conservation and low levels of remaining mangroves to deforest (Goldberg et al., 2020). In seagrasses, global estimates of habitat extent and loss are highly uncertain, ranging from 177,000 to 600,000 km$^2$ or higher (McKenzie et al., 2020), though Waycott et al. (2009) estimates an average 1.5% annual loss rate from 1990 to 2006. Dunic et al. (2021) likewise found that, from 1891 to 2018, seagrasses experienced an average decline of < 2% per year, but that loss rates were highly variable across regions. Finally, approximately 22% of coral reefs

![Fig. 1. Principal interactions between mangroves, seagrass, and reefs. Reefs, seagrasses, and mangroves buffer habitats further inland from storms and wave damage as well as participate in a tri-system exchange of mobile fish and invertebrates. Mangroves and seagrasses are critical in regulating sediment, freshwater, and nutrient flows to reefs.](image)
suffer from local stressors like nutrient pollution, while an additional 72% of reefs are affected by both local and global (e.g., ocean warming) stressors (Guan et al., 2020). To safeguard declining CMS, protected areas have been expanded to include at least 19% of mangroves and 27% of reefs worldwide (Chape et al., 2005; Burke et al., 2011), while the total portion of seagrass protected has, to our knowledge, not been reported. Seagrasses are often overlooked in marine conservation: by 2001, only 243 out of 4000 marine protected areas worldwide included seagrasses (Spalding et al., 2003), and a review of seagrass management plans in 20 regions worldwide revealed that existing conservation plans are lacking key elements such as cumulative impact assessments (Griffiths et al., 2020).

To examine the relationship between CMS, we first quantified their relative spatial overlap globally (Fig. 2). Coral reef and seagrass extent maps were acquired from the UN Environment Programme World Conservation Monitoring Centre (UNEP et al., 2010; UNEP-WCMC, 2016) and global mangrove extents from the 2016 release from the Global Mangrove Watch (Bunting et al., 2018). In this analysis, we used the UNEP World Conservation Monitoring Center Global Distribution of Seagrass dataset, which estimates the seagrass to cover 558,094 km$^2$ globally. This value is on the higher end of the estimated seagrass distribution globally (177,000 to 600,000 km$^2$).

Fig. 2. Locations where mangroves, reefs, and seagrass beds exist within 1 km of each other. (a) Buffered intersection between the three systems provides relative co-occurrence rates on a global scale. Regions where systems strongly intersect include Central America (Belize), the Caribbean, the Red Sea, the Coral Triangle (particularly Malaysia), Madagascar, and the Great Barrier Reef (b) Habitat intersection zones that occur within currently protected areas.
Table 1
Anthropogenic disturbances affecting mangrove, seagrass, and coral reef ecosystems. The source of each disturbance is noted alongside the results of disturbance, and potential protection resulting from the interaction between mangroves, seagrasses, and reefs.

| Land-sea ecosystem | Source of disturbance | Result of disturbance | Protection conferred by mangrove-seagrass-reef interactions |
|--------------------|-----------------------|-----------------------|------------------------------------------------------------|
| Mangroves          | Clear cutting         | • Aquaculture development is a major driver of mangrove loss (Ellegaard et al., 2014).<br>• Average loss of 0.18% per year of mangroves in southeast Asia (Richards and Friess, 2016).<br>• Cleared vs non-cleared mangrove sites show shifts in fish assemblages (Shinnaka et al., 2007).<br>• Rearrangement in species assemblages: cleared sites show more zooplanktivorous species compared to a greater component of benthic crustacean feeders found at mangrove sites (Shinnaka et al., 2007).<br>• Blue carbon markets from seagrasses and mangroves, and tourism in coral reefs and mangroves, can provide alternative sources of income to disincentivize clear-cutting (Spalding et al., 2017).<br>• Payments for blue carbon can result in greater profits than converting mangroves to shrimp farms (Yee, 2010). | |
| Sea level rise     |                       | • Low-lying islands are at the highest risk of SLR due to lack of sediment deposition (Gilman et al., 2007).<br>• Mangroves cannot migrate in areas with strong coastal development.<br>• In the absence of coastal squeeze (development barriers), mangroves may “back-step” into landward habitats (Saintilan et al., 2014; Di Nitto et al., 2014).<br>• Mangroves fringing larger landmasses and areas with significant river outputs are less vulnerable to SLR (McKee and Vervaeke, 2009).<br>• Mangroves at low tidal ranges are unlikely to grow at a sufficient rate, whereas mangroves at high tidal ranges are already positioned farther inland (Ward et al., 2016).<br>• Wave buffering from coral reefs and seagrasses can increase sediment trapping and accretion in coastal habitats (Alongi, 2008).<br>• Blue carbon storage potential of mangroves and seagrasses help offset carbon emissions (cause of SLR) (Alongi, 2012). | |
| Increased          |                       | • Warmer climates may allow mangroves to expand at latitudinal maxima (Alongi, 2015; Kelleway et al., 2017; Osland et al., 2017). However, poleward expansion may be inhibited by low habitat availability or dispersal barriers (Hickey et al., 2017).<br>• Rates of leaf photosynthesis for most species peak at temperatures at or below 30 °C, and leaf CO₂ assimilation rates of many species decline as temperature increases from 33 °C to 35 °C (Alongi, 2015).<br>• Blue carbon storage potential of mangroves and seagrasses help offset carbon emissions (cause of increased global and regional temperatures) (Alongi, 2012; Greiner et al., 2013). | |
| Extreme storms     |                       | • Hurricanes can alter mangrove stem size-frequency distributions and relative abundance, density (Smith et al., 2009).<br>• Some mangroves recover while others are converted to mud flats, with basin (rather than island) mangroves being the most vulnerable (Smith et al., 2009).<br>• Blue carbon storage potential of mangroves and seagrasses help offset carbon emissions mitigates damage from hurricanes and tropical storms, preventing phase shifts to mud flats (Alongi, 2008).<br>• Blue carbon storage potential of mangroves and seagrasses help offset carbon emissions (contributor of extreme climatic events) (Alongi, 2012; Greiner et al., 2013).<br>• Economic value of coastal ecosystems due to storm protection can be greater than economic benefits from degrading the system (Grabowski et al., 2012).<br>• Blue carbon markets from seagrasses and mangroves, and tourism in coral reefs and mangroves, can provide alternative sources of income to disincentivize dredging (Yee, 2010; Spalding et al., 2017). | |
| Dredging           |                       | • Fill material after mangrove clearing is often dredged from nearby reefs (Macintyre et al., 2009).<br>• Fill material after mangrove clearing is often dredged from nearby reefs (Macintyre et al., 2009). | |
| Marine and terrestrial debris |                       | • Mangroves can act as sinks for marine and terrestrial debris, mediating the impacts of marine and terrestrial debris on adjacent systems (Martin et al., 2019).<br>• Economic value of coastal ecosystems due to storm protection can be greater than economic benefits from degrading the system (Grabowski et al., 2012).<br>• Blue carbon markets from seagrasses and mangroves, and tourism in coral reefs and mangroves, can provide alternative sources of income to disincentivize dredging (Yee, 2010; Spalding et al., 2017). | |

(continued on next page)
| Land-sea ecosystem | Source of disturbance | Result of disturbance | Protection conferred by mangrove-seagrass-reef interactions |
|--------------------|-----------------------|-----------------------|----------------------------------------------------------|
| Pollutants         | • High inputs of untreated domestic sewage, storm water run-off, shipping effluent, and heavy metal contamination inhibit mangrove regeneration and growth (Defew et al., 2005).  
• Oil spills drive mangrove toxicity, algal blooms, and conversion to mud flats (Santos et al., 2012; Duke, 2016).  
• Seagrass communities reduce the amount of pathogens and bacteria in the water where adjacent systems show less impact from disease (Lamb et al., 2017; Sullivan et al., 2018). | • Seagrass communities reduce the amount of pathogens and bacteria in the water where adjacent systems show less impact from disease (Lamb et al., 2017; Sullivan et al., 2018). | |
| Invasive species   | • Introduction of two non-native mangrove species (Brugeria gymnorrhiza and Lumnitzera racemosa) in southern Florida have modified the structure and function of these mangrove forests (Carlton, 1989; Fourqurean et al., 2010).  
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• Hotels and coastal businesses may consider seagrasses an eyesore or nuisance. The need to preserve coral reefs (a tourism draw) can help justify seagrass protection (Daby, 2003).  
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• Economic value of coastal ecosystems due to storm protection can be greater than economic benefits from degrading the system (Grabowski et al., 2012). | |
| Seagrasses Removal | • Coastal development is a frequent cause of removal.  
• Area reduction of ~110 km² y⁻¹ since 1980; 29% of known seagrass beds have disappeared since they were initially recorded in 1879 (Waycott et al., 2009).  
• Hotels and coastal businesses may consider seagrasses an eyesore or nuisance. The need to preserve coral reefs (a tourism draw) can help justify seagrass protection (Daby, 2003).  
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| Increased turbidity | • Higher levels of turbidity results in lower irradiance, photosynthesis, and shoot density and growth. This drives lower sequestration of allochthonous blue carbon by seagrasses (Mazzarrasa et al., 2018).  
• Turbidity can increase the accumulation of allochthonous carbon and fine sediment particles (Mazzarrasa et al., 2018). | • Turbidity can increase the accumulation of allochthonous carbon and fine sediment particles (Mazzarrasa et al., 2018). | |
| Sea level rise     | • Sea level rise compresses seagrass habitats if not offset by sediment accretion, improvement in water clarity, and/or managed retreat from the coast (freeing up seagrass habitat). SLR may be responsible for a predicted 17% loss of seagrass habitat from 2000 to 2100 (Saunders et al., 2013).  
• Mangroves prevent sediment deposition, thereby improving water clarity. Seagrass persistence depends on water clarity under SLR; seagrasses may also migrate into mangrove habitats.  
• Wave buffering from coral reefs can increase sediment trapping and accretion in seagrasses (Guerra-Vargas et al., 2020).  
• Blue carbon storage potential of mangroves and seagrasses help offset carbon emissions (cause of increased global and regional temperatures) (Alongi, 2012; Greiner et al., 2013). | | |
| Increased temperatures | • Increase in water temperatures will depress photosynthetic rates and increase the amount of respiration (Short and Neckles, 1999).  
• Habitat contraction has already been noted and populations will begin to see drastic habitat incursion and species rearrangements as temperatures increase (Short and Neckles, 1999; Fraser et al., 2015).  
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• Blue carbon storage potential of mangroves and seagrasses help offset carbon emissions (cause of increased global and regional temperatures) (Alongi, 2012; Greiner et al., 2013). | |
| Extreme storms     | • Strong rainfall events could lead to mortality, and/or sediment accretion and seagrass growth. However, as sediment increases from rainfall and storm events, photosynthesis decreases and seagrasses experience widespread defoliation (Macreadie et al., 2019).  
• Wave buffering from coral reefs mitigates damage from hurricanes and tropical storms (Ferrario et al., 2014; Guannel et al., 2016).  
• Mangroves prevent sediment deposition.  
• Blue carbon storage potential of mangroves and seagrasses help offset carbon emissions (contributor of extreme climatic events) (Alongi, 2012; Osland et al., 2018).  
• Reducing additional pressure on native species is increasingly important. Mangrove-seagrass-reef interactions support nurseries and trophic redundancy for native species (Saenger et al., 2013). | • Strong rainfall events could lead to mortality, and/or sediment accretion and seagrass growth. However, as sediment increases from rainfall and storm events, photosynthesis decreases and seagrasses experience widespread defoliation (Macreadie et al., 2019).  
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• Reducing additional pressure on native species is increasingly important. Mangrove-seagrass-reef interactions support nurseries and trophic redundancy for native species (Saenger et al., 2013). | |
| Invasive species   | • At least 28 non-native species have become established in seagrass beds worldwide, of which 64% have documented or inferred negative effects (Orth et al., 2006).  
• Blue carbon storage potential of mangroves and seagrasses help offset carbon emissions (contributor of extreme climatic events) (Alongi, 2012; Osland et al., 2018).  
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• Reducing additional pressure on native species is increasingly important. Mangrove-seagrass-reef interactions support nurseries and trophic redundancy for native species (Saenger et al., 2013). | |
| Disease           | • Increased rates of disease are associated with warming temperatures (Sullivan et al., 2018).  
• Wave buffering from coral reefs mitigates damage from hurricanes and tropical storms (Ferrario et al., 2014; Guannel et al., 2016).  
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|                    |                       |                       |                                                          |
|                     |                       |                       |                                                          |
| Coral reefs         | Dredging              | • Sediments accumulate on living substrates. | • Mangroves can denitrify sewage effluent (Tam and Wong, 1999; Ouyang and Guo, 2016). |
|                    |                       | • Increases in turbidity and reduced light irradiance reduces coral calcification rates and can increase the prevalence of diseases (Pollock et al., 2014). | • Mangroves and seagrasses can absorb excess nitrogen (Adame et al., 2010). |
|                    |                       |                       | • Mangroves and seagrasses prevent heavy metal transport to coral reefs (Smith, 2018; Gopi et al., 2020). |
|                    |                       |                       | • Mangroves and seagrasses increase fish diversity, and may create ecological niche space for species threatened by invasives. |
|                    |                       |                       | • Mangroves and seagrasses prevent sediment deposition |
|                    |                       |                       | • Blue carbon storage potential of mangroves and seagrasses help offset carbon emissions (cause of SLR) (Alongi, 2012; Greiner et al., 2013). |
|                    |                       |                       | • Mangroves provide lower light environments for corals, reducing bleaching stress. |
|                    |                       |                       | • In particular, mangroves are alternative habitats (refuges) for coral species that thrive in low pH and high turbidity environments (Yates et al., 2014; Camp et al., 2016, 2019). |
|                    |                       |                       | • Mangroves enhance fish populations, dramatically increasing chances of ecosystem recovery (Munday and Hastings, 2007). |
|                    |                       |                       | • Mangroves and seagrasses serve as nursery habitats for diverse fish, buffering some negative effects of overfishing in reefs (Wakwabi, 1999; Crona and Rönnbäck, 2005; Saenger et al., 2013). |
|                    |                       |                       |                                                          |
| Sea level rise     |                       | • Sea level rise may increase turbidity and sediment levels and change wave dynamics, which decrease photosynthesis due to reduced light, and result in structural stress on coral reefs (Storlazzi et al., 2011; Baldock et al., 2014). | • Mangroves and seagrasses prevent heavy metal pollution |
|                    |                       |                       | • Mangroves and seagrasses can absorb heavy metal ions, for example, by precipitating sulfide minerals; absorbing and dissolving iron oxides; and binding soils (Attri and Kerkar, 2011). Mangroves thus prevent contaminant flows to ocean habitats. |
|                    |                       |                       | • Payments for ecosystem services (fishing, tourism, blue carbon) in mangroves, seagrasses, and reefs can provide alternative economic benefits, i.e., incentives against dredging (McKee and Vervaeke, 2009; Lau, 2013). |
| Increased          |                       | • Increases in mean sea surface temperatures and marine heatwaves has led to worldwide coral bleaching events (Brown, 1997; Burke et al., 2011). | • Mangroves and seagrasses prevent increased temperatures |
|                    |                       |                       | • In addition to severe mortality, bleaching events may lead to poleward range shifts in coral recruits and dominance of stress-tolerant species (Loya et al., 2001; Price et al., 2019). |
|                    |                       |                       | • Mangroves and seagrasses increase fish diversity, and may create ecological niche space for species threatened by invasives. |
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|                    |                       |                       |                                                          |
| Extreme storms     |                       | • In some cases, dramatic freshwater inputs into reef environments by storms or flooding events can negatively impact coral health and in extreme cases cause widespread mortality, particularly in larvae and juvenile corals. Effects are mediated by coral life history and morphology, site variables like depth, and other factors (Rogers, 1993). | • Mangroves enhance fish populations, dramatically increasing chances of ecosystem recovery (Munday and Hastings, 2007). |
|                    |                       |                       | • Mangroves and seagrasses serve as nursery habitats for diverse fish, buffering some negative effects of overfishing in reefs (Wakwabi, 1999; Crona and Rönnbäck, 2005; Saenger et al., 2013). |
|                    |                       |                       |                                                          |
| Overfishing        |                       | • Reduction in herbivores increases turf and macroalgae on coral reefs, often causing phase shifts from coral- to algal-dominated systems. | • Mangroves and seagrasses serve as nursery habitats for diverse fish, buffering some negative effects of overfishing in reefs (Wakwabi, 1999; Crona and Rönnbäck, 2005; Saenger et al., 2013). |
|                    |                       |                       | • Overfishing exacerbates coral mortality after bleaching events; healthy fish populations predict reef recovery (Graham et al., 2007; McClanahan et al., 2011). |
|                    |                       |                       |                                                          |
|                    |                       |                       |                                                          |
|                    |                       |                       |                                                          |
| 000 km²), where some of the seagrass populations in the dataset are not field validated (McKenzie et al., 2020). |
|                    |                       |                       |                                                          |
| To provide conservative estimators of ecosystem interactions, we buffered each ecotype by 1 km and mapped their intersection (i.e., 1 km proximities). The intersection of these three buffered areas totals 13,174 km² globally. Individually, the area of mangroves,
seagrasses, and reefs total approximately 136,000, 558,000, and 900,000 km², respectively, though reefs are frequently found far offshore and/or deeper than the coastal boundary. The boundaries of these three-system interaction zones were overlaid by the International Union for the Conservation of Nature (IUCN) protected area spatial dataset (UNEP-WCMC and IUCN, 2020) to quantify the extent to which these interactions are protected. Our analysis includes all habitat categories and levels of protected area in the IUCN dataset. While protected areas in this dataset represent different regulations, target organisms, and levels of enforcement, we chose not to restrict our analysis to specific protected area types. Protected area categories, limits, and enforcement levels are often undocumented or coded differently from country to country, and thus are impractical to filter. Based on this analysis, of the 13,000 km² of coastline where mangroves, seagrasses, and reefs interact, only 18% is currently designated as protected. It must be noted that the IUCN protected area dataset may underestimate areas managed by Indigenous Peoples and Local Communities (IPLCs), which manage or have tenure rights over at least ~38 million terrestrial km² worldwide (Garnett et al., 2018).

3. Causes of habitat degradation and disturbance

CMS are in decline globally due to a variety of anthropogenic disturbances (Table 1). While coastal habitats experience a wide variety of threats, below we highlight some of the most urgent and increasing pressures on these ecosystems: rising global temperatures, sea-level rise (SLR), deforestation and dredging, pollution, and invasive species.

Climate change is perhaps the most significant threat to coastal ecosystems worldwide. CMS are particularly vulnerable to rising temperatures and SLR, as many species already exist at their upper thermal limit (Lough et al., 2018) or deep range edge (Saunders et al., 2013). Mangrove populations may redistribute as air and water temperatures increase at their range limits, though mangroves show higher heat tolerance than many other plants (Waycott et al., 2011). At high latitudes, climatic warming may increase rates of photosynthesis and plant growth, while also reducing harmful frost events that present one of the greatest threats to mangroves (Cavanaugh et al., 2014; Sippo et al., 2018). Hickey et al. (2017) found no evidence of poleward migration in mangroves at 18 sites worldwide, though other studies (e.g., Saintilan et al., 2014) observed higher mangrove expansion and saltmarsh incursion at their latitudinal limits. Mangrove expansion is likely regionally dependent (Cavanaugh et al., 2018), and may be due to either settlement in new habitat, or return to areas that were previously depleted (Hickey et al., 2017). Variables that favor mangrove expansion include increases in annual minimum temperature and annual precipitation (Cavanaugh et al., 2018), as well as low elevation, wave sheltering, and high density of tidal creeks (Whitt et al., 2020). However, this expansion may be limited by dispersal barriers, like hydrodynamic forcing or sparse inland habitat, e.g., on atolls (Alongi, 2008; Di Nitto et al., 2014; Hickey et al., 2017). Interactions between ocean warming and SLR are uncertain: while some studies indicate that high temperatures may favor root growth sufficient to overcome SLR (Goldren et al., 2019), others predict that soil accretion and vertical growth rates will be unable to keep pace with SLR (Saintilan et al., 2020).

Ocean heatwaves have most conspicuously affected reef ecosystems; over 95% of the world’s reefs are expected to experience bleaching due to excessive temperatures by 2050 (Burke et al., 2011). Coral bleaching and mortality at the individual level can drive ecosystem-scale phase shifts, where other species and species groups can outcompete weakened corals for benthic habitat (McManus and Pol senberg, 2004; Hughes et al., 2007; Norstrom et al., 2009). Areas that exhibit bleaching resilience and resistance are associated with (1) decreased light stress, e.g., turbid reefs (Sully and van Woesik, 2020), (2) high currents and wave action (Nakamura and Van Wo esik, 2001), and (3) unique thermal features, e.g., reduced or variable temperature through upwelling or other cold-water plumes, or chronically high temperature in shallow lagoons or thermal pools (Coles and Jokiel, 1978; Palumbi et al., 2014). These conditions drive biophysical feedbacks, where physical controls on light and temperature can induce coral genetic expression and competitive selection for thermal tolerance (Barshis et al., 2013; Putnam et al., 2017). Corals may expand their home range under climate change (Yamano et al., 2011; Price et al., 2019), though SLR is expected to limit coral growth, particularly in turbid reefs (Morgan et al., 2020). Research comparing geospatial shifts in corals, seagrasses, and mangroves is critically needed, in order to predict novel interactions between these ecosystems.

The effects of rising temperature on seagrasses remain uncertain, but include decreased productivity, changes in morphology, reduced nutrient uptake, enhanced flowering, lower seedling performance, and range shifts (Short and Neckles, 1999). Increased water temperature decreases oxygen solubility and CO₂ leading to lower photosynthetic efficiency in seagrasses as well as photoinhibition from thermal stress and lower chlorophyll contents (Campbell et al., 2006; Staehr and Wernberg, 2009; Duarte et al., 2018). Epigenetic processes—e.g., DNA methylation, histone modification, chromatin remodeling, and small-interfering RNAs—may allow seagrasses to withstand climate change (Kelly et al., 2011; King et al., 2018). While understudied, epigenetics may be particularly important in seagrasses due to their partial clonal reproduction and low dispersal capacity, and thus relatively low genetic variation (King et al., 2018; Duarte et al., 2018). Range shifts in seagrasses will depend on light conditions, e.g., the balance of photosynthesis and respiration during, respectively, longer dark and light regimes of winter and summer at high latitudes (Duarte et al., 2018). Upslope shifts are expected under SLR (Valle et al., 2014) where coastal squeeze (human development) is absent, and ocean acidification may increase seagrass growth, since seagrasses are CO₂ limited (Koch et al., 2013; Burnell et al., 2014). Thus, the interactive positive/negative effects of climate change on seagrass cover is a critical area of research.

In addition to climate change, mangrove deforestation and reef and seagrass dredging have caused radical changes in these ecosystems. Removal and deforestation of mangrove forests peaked during the 1980s but still continues at a large scale today, particularly in southeast Asia (Shinnaka et al., 2007; El Legaa gd et al., 2014; Richards and Fries, 2016; Hamilton and Casey, 2016). The removal of mangroves often leads to an immediate influx of sediment into nearby habitats, damaging seagrasses and reefs. Mangrove removal can also reduce fish populations, preventing algal grazing, which leads to turfing, light shielding, and a decrease in reef and seagrass photosynthetic efficiency (Jaxion-Harm and Speight, 2012). In addition, when mangroves are removed, fill material is often dredged...
from nearby reefs (Macintyre et al., 2009), and redistributing dredged material causes high soil degradation and erosion in newly filled areas (McKee and Vervaeke, 2009). Reef dredging also resuspends fine particles in the water column, reducing light availability before resettling on benthic organisms (Brown, 1997; Pollock et al., 2014). This sudden increase in turbidity and reduced light irradiance reduces coral calcification rates and can increase the prevalence of diseases (Bak, 1978; Pollock et al., 2014). Mangrove and seagrasses are strong carbon sinks, and their removal releases substantial carbon into the atmosphere, e.g., 0.29–3.9 Tg CO$_2$ yr$^{-1}$ in Mexico from mangrove deforestation (Adame et al., 2018b). In addition, by remobilizing sediment, dredging can release carbon that has accumulated in the benthos over thousands of years (Duarte et al., 2013, 2018).

Major pollutants such as oil spills, heavy metal contamination, and marine debris cause long-term damage to the coastal matrix. Here, we focus on oil spills; reviews on other forms of pollution like sediment runoff can be found in Fabricius (2005) in reefs, Maiti and Chowdhury (2013) in mangroves, and Short and Wyllie-Echeverria (1996) in seagrasses. Strong uncertainty exists on oil spill impacts. In seagrasses, case studies in San Francisco Bay and Gladstone, Australia show no impact of oil spills on shoot densities, reproduction, rhizome elongation, and photosynthetic efficiency (Fonseca et al., 2017), and no effect on biomass, density, and area (Taylor and Rasheed, 2011). One experiment showed short-term seagrass resilience to oil but increased mortality after 5 h of exposure (Thorhaug et al., 1986), though in another study, seagrasses rebounded after 4 days (Macinnis-Ng and Ralph, 2003). Coral reefs and mangroves are oil sensitive, and oil spills have caused sharp declines in coral cover and diversity, particularly in branching species like *Acropora* sp. (Guzmán et al., 1991). At least 238 oil spills have affected up to 1.94 million ha of mangrove habitat since 1958, killing 126,000 ha of mangroves (Duke, 2016) and driving phase shifts to tidal flats (Santos et al., 2012). Oil spills may also cause algal blooms that smother seagrasses and corals, perhaps by killing herbivores (Jackson et al., 1989; Jacobs, 1980; Ralph and Burchett, 1998). A possible solution lies in the use of bioremediation (novel bacterial consortia) to degrade oil while preserving beneficial coral microbiomes (ados Santos et al., 2015).

Non-native species alter CMS species assemblages and ecosystem function (Carlton, 1989). For example, in South Florida, the introduction of two non-native Indo-Pacific mangrove species (*Brugiera gymnorrhiza* and *Lumnitzera racemosa*) modified the cycling of the detrital material in local mangroves, and the Brazilian pepper *S. terebinthifolius* produced noxious secondary compounds that depressed mangrove seedling growth (Fourqurean et al., 2010). In reefs, invasive species may amplify other, overlapping threats. For example, in the Bahamas, an invasive lionfish led to a reduction in herbivores, resulting in increased algal cover at mesophotic (30–150 m) depths, which in some regions serve as bleaching refugia (Lesser and Slattery, 2011). In seagrasses, herbivores are generally important for soil quality and oxygenation, but invasive herbivores can lead to overgrazing and a loss of both autochthonous and allochthonous carbon storage (Eklöf et al., 2008; Mazarrasa et al., 2018). In addition, non-native species in mangrove and seagrass habitats negatively impact reef fish biomass (Mumby et al., 2004; Albins and Hixon, 2008; Unsworth et al., 2008).

4. Conservation efficiencies between coral reef, mangrove and seagrass ecosystems

Confronting increasing ecosystem threats requires strategic conservation, and in recent years, land-sea conservation has attracted increasing attention as a critical priority (Alvarez-Romero et al., 2015; Jupiter et al., 2017; Delevaux et al., 2018). In particular, jointly protecting mangroves, seagrasses, and reefs may synergistically increase the benefits of conservation due to positive feedbacks at habitat boundaries. An “edge” or “boundary” is defined as the interface between two adjacent types of habitat (Strayer et al., 2003) where the boundary possesses unique abiotic conditions (e.g., temperature, light) that are different from the adjacent habitats (Ewers and Didham, 2006). Species associated with CMS migrate between adjacent coastal habitats for reproduction, sheltering, and predation, producing unique species interactions and supporting heterogeneous assemblages along habitat edges (Fagan et al., 1999; Fletcher et al., 2007). These ecosystem interactions are not restricted to the interface, and spillover effects of each system can impact other ecosystems kilometers away (Mumby et al., 2004), mediated through factors such as habitat extent, patchiness, and currents (Olds et al., 2012).

The role of boundary habitats in promoting resilience to threats, such as those noted above, has received little attention in previous literature. However, based on our review of CMS interactions, we find that boundary habitats may achieve the following conservation efficiencies:

1. **Increase resistance to disturbance**: Create structural support against, or buffer the flow of, external stressors such as pollutants and wave energy.
2. **Support high diversity and connectivity**: Support species at multiple life history stages and trophic levels within a relatively small geographic area.
3. **Habitat portfolio effects**: Provide refugia for species displaced by destruction; these newly occupied habitats may be functionally similar to lost habitats, or support only certain species.
4. **Create incentives against destruction**: Build ecosystem services as financial disincentives to harmful human activities.

Below, we outline interactions between CMS ecosystems, highlighting processes by which these boundary habitats may promote conservation synergies. This synthesis demonstrates how ecosystem feedbacks may naturally amplify conservation benefits where CMS are jointly protected.

4.1. **Increase resistance to disturbance**

“Resistance” refers to the ability of individual organisms to experience disturbance without undergoing dramatic change (e.g.,
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mortality) (West and Salm, 2003). Resistance may arise from an individual’s intrinsic, physiological tolerance, or from habitat conditions that buffer stress (Done, 1999; West and Salm, 2003). Interactions between CMS create conditions for resistance by decreasing the magnitude of disturbance across ecosystem boundaries.

Reefs, which consist of highly complex calcareous structures, are effective barriers against the erosive impact of waves and currents on shoreline habitats, creating low-energy environments that are favorable for mangrove and seagrass growth (Ogden and Gladfelter, 1983; Lowe, 2005). Seagrasses further attenuate wave damage, and the reef-seagrass matrix has been shown to reduce wave height and minimize mangrove floor erosion (Guannel et al., 2016). As a result, offshore ecosystems protect increasingly nearshore systems from storm surge and wave damage (Chen et al., 2007; McIvor et al., 2012; Ferrario et al., 2014; Ondiviela et al., 2014; Guannel et al., 2016). The extent of protection may depend on local factors like reef geomorphology. For example, in simulations of a fringing reef, corals provided greater wave protection than seagrasses, while in a barrier reef, seagrasses provided greater wave protection than corals and compensated for coral loss (Guannel et al., 2016).

In addition, transpiration in mangrove forests reduces the flow of freshwater to the ocean, mitigating damage from heavy rainfall events. By buffering freshwater flows, mangroves regulate salinity fluctuations in seagrasses and coral reefs (Theuerkauff et al., 2018). In addition, mangroves and seagrasses bind sediment (Amoudry and Souza, 2011; Volpe et al., 2011; Stutter et al., 2017), protecting adjacent reefs from sediment burial and preserving water clarity during storm events (Boynton et al., 1980; Schaffelke et al., 2012; Warrick et al., 2004). Water clarity also helps reefs and seagrasses build resistance to SLR, because benthic organisms can survive in deeper water if light access and resulting productivity remains high (Saunders et al., 2013). It must be noted that the amount of sunlight received by corals and seagrasses is not only influenced by sediment, but by colored dissolved organic matter (CDOM), phytoplankton, and non-algal particles (Mobley, 1995; Babin et al., 2003; Lee, 2006; Li et al., 2019a), which mangroves may increase (Jaffé et al., 2004; Shank et al., 2010; Safiullah et al., 2016). The geomorphology of both mangroves and reefs affects where and how much sediment is distributed at the coastal margin. For example, riverine rather than tidal mangroves create a more homogenous spread of coastal sediment across the intertidal zone (Adame et al., 2010). In addition, mangroves may be insufficient barriers against sediment on reefs where upstream land use is extremely erosive (Victor et al., 2004), or in large and steep catchments.

CMS also generate distinct biogeochemical conditions that can buffer the effects of ocean acidification and pollution. Ocean acidification is a major threat to corals, and occurs when dissolved pCO₂ binds with carbonate that is required to build coral skeletons, while also reducing seawater pH (Hoegh-Guldberg et al., 2007). Seagrasses exhibit higher mean pH and reduced pCO₂ than surrounding habitats, and therefore may increase the saturation state of aragonite and enable downstream coral reefs to sustain positive calcification rates (Camp et al., 2016). The role of mangroves as a buffer is more uncertain: mangroves in the Caribbean, Seychelles, and Indonesia exhibited lower pH and higher pCO₂ than a nearby outer-reef (Camp et al., 2016), while in the U.S. Virgin Islands and western Australia, mangroves created a localized increase in ocean pH (Yates et al., 2014; Sippo et al., 2016). The relationship between dissolved inorganic carbon, total alkalinity, and calcification in coastal ecosystems likely varies both regionally and according to diel cycles of photosynthesis and respiration. However, there is evidence that either seagrasses, mangroves, or both can offset acidification in reefs.

In regions with severe pollution stress, mangrove soils have the ability to retain heavy metals, reducing the amount of toxins leaching from soils into coastal waters (Tam and Wong, 1999; Attri and Kerkar, 2011; Ouyang and Guo, 2016). Metals like copper, lead, and zinc accumulate in mangrove roots and leaves (MacFarlane et al., 2007), or lose bioavailability through precipitation as sulfides or complexation with organic matter in anoxic, detritus-rich sediment (MacFarlane et al., 2003). Nonetheless, the longevity of mangroves as a sink for heavy metals may depend on the type of soil and type of metal (Tam and Wong, 1996), and mangrove senescence may remobilize metals (Almahasheer et al., 2018). In addition to heavy metals, mangroves and seagrasses buffer excess nitrogen, which can impede coral growth and accelerate coral bleaching (Morell and Corredor, 1993; Donovan et al., 2020; Adame et al., 2018a). For example, in Puerto Rico, mangrove sediment-microbial communities were capable of denitrifying 10–15 times the nitrate levels of effluent from the local sewage treatment plant (Corredor and Morell, 1994). Conversely, mangrove litter, benthic algae, and seagrasses are net sources of autochthonous dissolved organic carbon (DOC) (Kristensen et al., 2008; Maher et al., 2013; Barrón et al., 2014). While Odum (1968) hypothesized that coastal ecosystems are a major source of offshore carbon, carbon subsidies depend on “trophic relay” by mobile organisms that migrate in and offshore between seagrasses and mangroves (Walton et al., 2014).

In sum, CMS reduce disturbance from large storms, SLR, pollution events, and ocean acidification in adjacent systems. By absorbing the magnitude of biophysical flux across habitat boundaries, coastal ecosystems provide structural stability to nearby habitats. Seagrasses may be especially critical in these positive feedbacks, as they offer bidirectional benefits in the form of wave attenuation and sediment filtration to both mangroves and coral reefs. However, it must be noted that, even when protected, these ecosystems are likely to redistribute as ocean heatwaves, SLR, large storms, and acidification increase. Coastal interactions between redistributed ecosystems is a critical area of ongoing research.

4.2. Support high diversity and connectivity

A central goal of many conservation efforts is to safeguard biodiversity during the sixth mass extinction (Dinerstein et al., 2019). Maintaining marine biodiversity supports ecosystem sustainability, functionality and productivity (Loreau et al., 2001; Heiskanen et al., 2016). Indicators of biodiversity span various levels, from genes to species functional roles to ecosystems, although species richness is a common metric (Magurran and McGill, 2011). Reduction in biodiversity can impact productivity, disease dynamics and stability in the face of climate change (Loreau et al., 2001; Duffy and Stachowicz, 2006). For example, highly diverse benthic assemblages (including corals, sponges and macroalgae) are more resistant to ocean acidification, as high biodiversity increases food availability and supports beneficial microorganisms (Rastelli et al., 2020). Generally, biodiverse communities show higher resilience, as
greater diversity increases the chance that a species is present that is suited to altered conditions, providing a buffer for species loss, or reducing the chance that the ecosystem will be compromised (Folke et al., 2004). Therefore, high-biodiversity regions with higher functional redundancy are more likely to remain more stable under anthropogenic change and should be prioritized as regions to conserve (Oliver et al., 2015; McWilliam et al., 2018).

Prior research indicates that coastal ecosystems harbor exceptional biodiversity within relatively small geographic areas. Mangroves, seagrasses, and reefs are highly productive, generating gradients of resource availability that support biodiversity (Alongi, 2012). Coastal species richness far exceeds pelagic richness as a result of greater habitat heterogeneity through topographic and temperature variation at the coast (Angel, 1993; Costello and Chaudhary, 2017). Mangroves and seagrasses support species across terrestrial, marine, and anadromous taxa, including birds, mammals, insects, reptiles, tunicates, sponges, bivalves, algae, cnidarians, and fish (Nagelkerken et al., 2008). Coastal biodiversity increases through high connectivity: for example, coral reefs in mangrove-rich regions in Belize (Mumby et al., 2004) and Australia (Henderson et al., 2017) showed significantly higher fish biomass and species richness, respectively, than reefs in mangrove-sparse regions. Similarly, seagrasses increased adult fish diversity in Indo-Pacific reefs (Dorenbosch et al., 2005), with continuous and non-patchy seagrass beds showing highest benefits to beta diversity (Henderson et al., 2017).

One way that mangroves and seagrasses support biodiversity is by serving as important nurseries for migratory fish. A nursery can be defined as an area where juvenile density, growth, survival, and movement to adult habitats is greater than in other habitats (Beck et al., 2001), which has been empirically validated for coastal vegetation (Lefcheck et al., 2019). The large surface areas afforded by complex mangrove root structures and pneumatophores, or aerial roots, fosters complex biofilms and a range of epiphytic algae producing ample food for nursery fish (Saenger et al., 2013). In addition, mangroves and seagrasses provide juveniles with a sheltered environment, and physically intercept and concentrate planktonic larvae (Saenger et al., 2013). Since seagrass beds often occur as extensive, continuous beds compared to patchy reefs, (Sweatman and Robertson, 1994), competent larvae will encounter seagrasses more frequently than coral and therefore use seagrasses as a “waiting room” before migrating to the reef (Parrish, 1989). Mangroves and seagrasses have a huge impact on the survival and recruitment of many juvenile species, such as the spiny lobster (Panulirus argus), the commercially important pink shrimp (Penaeus duorarum), and snapping shrimp from the genus Lutjanus (Crona and Rønning, 2005). Numerous species, including many commercially important fish, migrate offshore later when the mangrove or seagrass roots can no longer provide sufficient shelter for their size (Nagelkerken et al., 2000; zu Ermgassen et al., 2020). Change in diet may also be responsible for ontogenetic habitat shifts from mangroves and seagrasses to coral reefs (Cocheret de la Morinière et al., 2003).

In addition, CMS generate resources for multiple trophic levels by facilitating sheltering and predation. The migration of juveniles from seagrasses and mangroves attract larger predatory reef fishes such as redfish and tarpon, which are known to forage along mangrove fringes (Ogden and Gladfelter, 1983; Wakwabi, 1999). Adult prey species migrate into mangroves during periods of tidal inundation, when the higher levels of turbidity found in mangroves obscure prey, and mangrove roots and pneumatophores provide structural protection (Abrahams and Kattenfeld, 1997; Huxham et al., 2004). On the other hand, fish such as seabream and gray snapper avoid the “risky” mangrove-seagrass zone to avoid predators, although the highest food abundance is within this zone (Hammerschlag et al., 2010). Thus, the foraging behavior of prey fish is species specific, and likely depends on factors such as predator avoidance, structural complexity, and shade (Cocheret de la Morinière et al., 2003). The tradeoff between food and shelter is evident in the “halo” effect, where patch reefs adjacent to seagrass beds are bordered by a diameter of cropped seagrass cover (Hay, 1984). This is caused by grazing of animals such as sea urchins and parrotfish, which venture out of the reef front to forage, but only to a limited extent to avoid predation (Ogden et al., 1973).

In sum, coastal ecosystems form centers of high productivity, where closely linked habitats serve multiple ontogenetic stages of predators and prey. Coastal boundaries provide species with many options for reproducing, sheltering, and feeding within small geographic areas, accessible at low energetic expenditure compared to high-seas migrations. Boundary habitats provide mobile organisms with access to spatially separated resources, e.g. nesting occurs in one site while foraging occurs in another (Gates and Gysel, 1978; Fagan et al., 1999; Ries et al., 2004; Fletcher et al., 2007). Joint protection of coastal ecosystems therefore captures a key conservation efficiency: the ability to protect significant ecosystem connectivity and gene flow over a relatively small area.

4.3. Habitat portfolio effects

The concept of ecological portfolio effects captures the protective function of overlapping ecological assets, which can include genes, species, functional roles, or ecosystems (Figege, 2004; Schindler et al., 2010; Bråthen and Lortie, 2016). In the context of coastal ecosystems, when one habitat is disproportionately impacted by stress, alternative habitats in close proximity may provide refugia to mobile organisms. The outcome of this process may be rearrangements in species, including encroachment into new habitat (Loarie et al., 2009), which can lead to competitive interactions but also avert total species loss. In particular, the tight connectivity between CMS may allow these ecosystems to host displaced species.

One example of this process is the emergent role of mangroves and seagrasses as climate refugia for coral reefs. Several studies have found diverse coral species growing on or around mangrove roots after bleaching events (Yates et al., 2014; Camp et al., 2019), with mangrove-associated corals bleaching at significantly lower rates than exposed corals (Yates et al., 2014; Rogers, 2017). For example, over 30 species of corals were documented in mangrove refugia in the USVI, exhibiting lower bleaching than high-light and lower-temperature conspecific outside of mangroves (Yates et al., 2014; Rogers, 2017). Mangroves may create refugia by providing shade and reducing symbiont photo inhibition, and by offering habitat under high and variable temperatures where reefs acclimate to thermal anomalies (Oliver and Palumbi, 2011; Van Woesik et al., 2012; Palumbi et al., 2014). Corals in mangroves have been seen to change dominant Symbiodiniaceae taxa and exhibit higher levels of heterotrophy, which can, respectively, improve thermal tolerance
and help corals offset photosynthetic losses during bleaching (Camp et al., 2019). While coral refugia in mangroves have only been identified in a few case studies, e.g., in the USVI (Yates et al., 2014; Rogers, 2017), Great Barrier Reef (Camp et al., 2019), Seychelles, and Indonesia (Camp et al., 2016), certain coral species (e.g., stronger heterotrophs) appear to inhabit mangroves more than others, and the community ecology of coral refugia requires further research. Mangroves serve as refugia for reef fish as well; in one study of degraded reefs where habitat complexity was reduced, mangrove nurseries supported fisheries productivity equal to, or greater than, complex reefs that lacked nurseries (Rogers and Mumby, 2019). Seagrasses may also serve as refugia for corals under ocean acidification. For example, in the Cayman Islands, 14 coral taxa recruited into seagrass beds, despite low availability of hard substrate (Lohr et al., 2017).

Increases in global temperatures, SLR, and rainfall may allow for the encroachment of mangroves and seagrasses into other coastal habitats (see “Causes of habitat degradation and disturbance”). Native salt marsh habitats have been particularly susceptible to mangrove encroachment (Sippo et al., 2018). As mangroves expand into salt marshes, they are expected to increase nutrient storage and reduce storm damage, but threaten large migratory birds like the whooping crane and foraging bats that depend on open vegetal structures (Kelleway et al., 2017). The incursion of woody plants into herb-dominated marshes can alter root productivity, decomposition processes, carbon cycling, sediment accretion, and below-ground carbon storage, for example, by increasing root production (Yando et al., 2018; Coldren et al., 2019). However, these effects are still uncertain and, likely, regionally dependent (Cavanaugh et al., 2018).

In many cases, the ecological effects of species range shifts have yet to be seen. However, protecting a portfolio of interconnected coastal ecosystems (i.e., mangroves, seagrasses, and coral reefs together) may help safeguard future refugia and offset wholesale species loss during the Anthropocene.

4.4. Create incentives against destruction

Vegetated coastal habitats are ranked among the most economically valuable in the biosphere (Costanza et al., 1997). CMS provide immense ecosystem services to human communities, which amplify as these ecosystems interact. Ecosystem services may provide economic incentives against harmful human activities, such as mangrove deforestation. Multiple coastal ecosystems should be protected together in order to maximize ecosystem services, since safeguarding one ecosystem service may inherently bolster others. In previous studies, when the ecosystem services of reefs, mangroves, and seagrass beds were all incorporated into coastal planning, the supply of these services was much greater than when one ecosystem alone, or a combination of two, were considered (Arkema et al., 2015). Below, we outline several synergies between ecosystem services in CMS (Fig. 3). We highlight fisheries, tourism, carbon storage, and coastal protection as services that have catalyzed changes in conservation practices, and exhibit clear synergies.

CMS provide significant coastal protection by reducing coastline erosion, attenuating storm surges and non-storm waves, and mitigating floods (Bridges et al., 2013). Approximately 40% of the world’s population lives within 100 km of a coast (Small and Nicholls, 2003), 40% of which benefit from nature-based coastal protection (Van Coppenolle and Temmerman, 2018). Mangroves

![Diagram](image_url)

**Fig. 3.** Ecosystem service synergies between mangroves, seagrasses, and reefs. The ecosystem services provided by intact reefs, seagrasses, and mangroves are both highly valuable and mutually enhance each other. Coastal protection (storm/wave attenuation) maintains the structure of adjacent ecosystems, and associated ecosystem services, in an offshore-to-onshore direction. Fisheries are characterized by migratory species, and therefore, protecting fisheries in one ecosystem increases fish biomass in others. Tourism benefits from coastal protection and healthy fisheries from multiple ecosystems. Here, we do not draw within-ecosystem connections in order to better emphasize synergies between systems.
(McIvor et al., 2012), reefs (Ferrario et al., 2014; Guannel et al., 2016), and seagrass beds (Chen et al., 2007; Ondiviela et al., 2014; Guannel et al., 2016) all mitigate coastal hazards and are more cost-effective than alternative, built-or “gray infrastructure” coastal hazard reduction strategies (Temmerman et al., 2013). As a result, the economic value of coastal ecosystems due to storm protection can be greater than economic benefits from destructive forms of harvesting of the same region (Grabowski et al., 2012). Storm attenuation by each ecosystem keeps adjacent habitats intact, and therefore, coastal protection in mangroves, seagrasses, and reefs builds synergistically (Fig. 3). In addition, fishing industries worldwide are highly dependent on mangroves, seagrasses, and reefs, and coastal ecosystems support 95% of commercial fish species (Janes et al., 2020b). Coral reefs supply 5.7 billion dollars of fish globally (Cesar et al., 2003), and mangroves in Indonesia and Mexico yield $24.3 and $1394/ha/year, respectively (Hutchison et al., 2014). Seagrass habitats are less studied but highly valuable; for example, seagrasses in Queensland and Gran Canaria produce fisheries worth $974 and $1500/ha/year (Tuya et al., 2014; Unsworth et al., 2010). A recent comparison of vegetated and bare seabed in Australia showed that seagrass sequestered ~$17,000/ha in commercial fish, while mangroves provided $15,000/ha and tidal marshes created $1300/ha (Janes et al., 2020b), contributing a total of ~$600 million to Australia’s fisheries (Janes et al., 2020a). In many regions, mangroves have been converted to shrimp farms, but intact mangroves have greater economic value to local communities than shrimp farms as they support offshore fisheries and supply wood products (Sathirathai and Barbier, 2001; Gunawardena and Rowan, 2005). As noted, many fish species rely upon all three ecosystems at various life-history stages for spawning, shelter, and feeding (Ogden, 1988). Thus, protecting fisheries in one ecosystem can increase fish stocks and economic value in others (Fig. 3).

Tourism offers an alternative source of income for communities implementing CMS protection. In reefs, tourism expenditures are estimated at $3.8 billion annually (Spalding et al., 2017). Tourist activities can disrupt and degrade reefs (Gil et al., 2015); however, tourism has also been a successful means of community-based protection of marine resources (Brunnschweiler, 2010). While less lucrative, mangrove tourism is a valuable industry in some regions (Miranda et al., 2013), with mangrove tourist attractions spanning 4000 locations across 93 countries (Spalding and Parrett, 2019). In contrast, seagrasses are seldom commodified, and are instead dredged by hotels who consider seagrass an eyesore (Daby, 2003). Strong synergies exist between tourism and other ecosystem services (Fig. 3). Coastal facilities for reef tourism (e.g., hotels) benefit from storm protection by CMS. Reef tourism depends directly on conserving healthy fisheries across all coastal ecosystems.

Critically, blue carbon in mangroves and seagrasses represents a promising source of income to communities where carbon offset programs exist (Albert et al., 2012; Locatelli et al., 2014). Coastal ecosystems cover only 3% of the area of terrestrial forests, yet bury a similar amount of organic carbon per year as forests (Duarte et al., 2013). For example, mangroves bury 163 g m$^{-2}$ of Corg per year and hold a soil carbon stock of up to 683.4 Mg Corg ha$^{-1}$ (Duarte et al., 2013), vastly exceeding the storage efficiency of tropical forests (McLeod et al., 2011). Coastal vegetation is a particularly strong carbon sink because of its high productivity, as well as high efficiency in trapping and continually accreting sedimentary carbon (McKee et al., 2007; McLeod et al., 2011; Duarte et al., 2013). Coastal conservation leads to twofold carbon sequestration, both by enhancing carbon storage through vegetal growth and preventing remineralization of existing soil carbon that builds up over millennia (Macreadie et al., 2019). Climate change will likely alter existing carbon stocks, both positively and negatively: for example, large storms can drive carbon loss from sediment resuspension and canopy damage, but increase carbon storage through sediment accretion (Macreadie et al., 2019). A key question is whether habitat productivity and landward encroachment will keep pace with SLR. A recent analysis found that wetland increases of up to 60% are possible under climate change (Schuerch et al., 2018), if human communities take action to safeguard corridors of landward growth (Lovelock and Reef, 2020).

There is strong evidence that blue carbon amplifies through protection in nearby ecosystems. Climate change may enhance blue carbon if mangroves and seagrasses are able to migrate landward. Therefore, reducing human disturbance inland can preserve novel habitat for coastal species. In addition, protecting storm buffers like coral reefs can prevent wave damage and erosion in blue carbon reservoirs (Guannel et al., 2016) while allowing mangroves and seagrasses to accrete through sediment subsidies from large storms (Macreadie et al., 2019). For example, in seagrass beds, organic carbon in sediments was 144 Mg ha$^{-1}$ and 91 Mg ha$^{-1}$ where seagrasses were, respectively, sheltered and unsheltered by barrier reefs (Guerra-Vargas, 2020). Numerous international and domestic frameworks have been proposed to enhance blue carbon (see “Management strategies and challenges”), offering substantial economic opportunities to incentivize large-sea conservation.

In sum, the ecosystem services provided by intact CMS are both highly valuable and mutually enhance each other. Ecosystem services offer opportunities to make conservation economically viable, and provide novel sources of income to disincentivize human activities threatening coastal species. The high connectivity in land-sea ecosystems leads to synergistic gains, where improving one ecosystem service inherently augments others.

5. Management challenges and strategies

Despite clear benefits of land-sea management, many physical and sociopolitical barriers exist. Land-sea conservation is often perceived as primarily benefiting corals, the downstream endpoint of protection, leading to one-sided leadership from the marine realm (Stoms et al., 2005; Carlson et al., 2019). In addition, few conservation planners have access to spatial and temporal data on land-sea processes (Alvarez-Romero et al., 2011), making it difficult to define relevant scales of joint management (e.g., stream order and reef extent) (Jupiter et al., 2017). Many governments are organized into explicitly terrestrial or marine realms, which operate under legal mandates that do not prioritize integration and drive budgetary competition rather than coordination (Fiorino and Fiorino, 2006; Adams et al., 2014). Moreover, performance metrics and values targeted by land and sea managers may differ. For example, conservation areas that maximize terrestrial biodiversity or improve marine water quality do not necessarily overlap, resulting in
disagreements over conservation siting (Makino et al., 2013; Álvarez-Romero et al., 2015).

Existing efforts to conserve mangroves, reefs, and seagrasses take on many forms (no-take zones, time-area closures, etc.), and are frequently organized into protected areas, i.e., Marine Protected Areas (MPAs) or Terrestrial Protected Areas (TPAs). Conservationists have increasingly called for the expansion of protected areas across 30–50% of reefs (McLeod et al., 2009) and at least 50% of terrestrial areas (Dinerstein et al., 2019) as a “Global Safety Net” to sustain biodiversity and enhance carbon drawdown worldwide (Dinerstein et al., 2020). There is strong evidence that protected areas fail to benefit ecosystems if functional connectivity is not adequately taken into account (Jones, 2002). In particular, MPAs suffer from insufficient protection at the land-sea interface and provide decreased benefits to corals in heavily sedimanted areas. For example, in the U.S. Virgin Islands and Solomon Islands, there was no significant difference in coral cover between fished and non-fished areas, perhaps due to sediment loading from deforestation and land use change upstream (Stoms et al., 2005; Begin et al., 2016). More dramatically, reserve areas in the Great Barrier Reef showed significantly lower coral cover than fished areas after repeat flood exposure (Wenger et al., 2016). However, when target species are herbivorous, reserves appear to benefit coral recovery from flooding, particularly on reefs near mangroves (Olds et al., 2014). Finally, while MPAs normally provide protection against coral disease, poor water quality negates these benefits (Lamb et al., 2014). Given the significant political and financial capital ($5–19 billion per year globally) required to establish MPAs, stronger management of connected ecosystems is necessary to ensure MPA efficacy (Balmford et al., 2004).

Numerous management strategies have been proposed to link land and sea conservation, including the framework of Integrated Coastal Zone Management (ICZM). ICZM arose during the 1960–70s to negotiate increasingly private claims to coastal spaces which, prior to development, were governed by a common property or open access doctrine (Forst, 2009). Numerous countries around the world have adopted ICZM legislation over the past several decades, including the United States’ Coastal Zone Management Act of 1972 and Belize’s Coastal Zone Management Act of 1998 (Gibson et al., 1998; Beatley et al., 2002). These laws require national or sub-national entities to create Coastal Zone Management Plans, which typically hybridize conservation with urban planning goals. For example, in the United States, coastal states receive grants under ICZM to protect public access to beaches, reduce shoreline erosion, and identify permissible land and water uses, among other objectives (Beatley et al., 2012). ICZM programs are often implemented by planning and zoning rather than environmental agencies, and therefore may not coordinate with MPA and TPA authorities. Another common pitfall to ICZM is scientific research bottlenecks, where coastal research is too fragmented or piecemeal to be readily used by decision makers. Building interdisciplinary research programs like Cooperative Research Centers and multi-stakeholder institutions with joint decision-making authority can be critical to integrated governance (Shipman and Stojanovic, 2007; Jupiter et al., 2013).

Island communities represent a special case of CMS connectivity and governance. On many islands, feedback loops between land-sea ecosystems are especially tight and impacts of disturbance are fundamentally transboundary (Jenkins et al., 2010; Jupiter et al., 2014), and while government capacity is often low on islands, strong community-based institutions exist (Clarke and Jupiter, 2010). Integrated Island Management (IIM) proposes guidelines for advancing joint land-sea conservation on islands specifically, while also drawing from the elements of other well-used management frameworks (such as ICZM, Ecosystem-Based Management, and Integrated Water Resources Management) (Jupiter et al., 2013).

IIM solutions emphasize community inclusion into planning and decision-making, especially where indigenous ridge-to-reef management can unify overlapping state jurisdictions (e.g., vañua system in Fiji, puava in Solomon Islands). Steps for empowering local decision-makers include recognizing indigenous systems through national legislation, reinforcing the roles of indigenous leaders, defining and recognizing marine and land tenure claims, prioritizing participatory planning methods, creating information-sharing networks across decentralized community groups, and establishing sustainable funding sources (e.g., through tourism user fees, community trusts, and occasionally private-sector partnerships) (Clarke and Jupiter, 2010; Jupiter et al., 2013). At an international level, the IUCN has begun to formally recognize indigenous management areas as an alternative to national Protected Areas under the status of Other Effect Area-Based Conservation Measures (OECM). For case studies of successful land-sea management and a full explanation of IIM principles, see Jupiter et al. (2013, 2014, 2017).

Blue carbon has gained significant momentum as a market-based approach to systematic land-sea conservation. Under the Paris Agreement, countries can include blue-carbon sequestration as a Nationally Determined Contribution to lowering emissions, and the United National Framework Convention on Climate Change (UNFCCC) offers two mechanisms for carbon trading: the Reduced Emissions from Deforestation and Degradation (REDD+) program (Yee, 2010; Lau, 2013; Ahmed and Glaser, 2016) and the Clean Development Mechanism, though these only include mangroves at present (Thomas, 2014). Voluntary carbon markets and organic certification standards can support smaller-scale projects, and have lower transaction costs but offer lower carbon credit prices than UNFCCC methods (Wylie et al., 2016). Voluntary projects have been used to fund school construction and water infrastructure, supporting alternative livelihoods for local women (Plan Vivo, 2015), and can generate greater profits than destructive shrimp farms (Yee, 2010). Importantly, plans to apply REDD+ and similar payment tools should ensure that payments benefit community-level actors, especially where community land/marine tenure has not been formally recognized. Possible future geographies for blue carbon markets include Indonesia, Brazil, Malaysia, and Papua New Guinea, which represent about 50% of the global mangrove carbon stock (Goldberg et al., 2020).

Viable management actions to protect CMS and boost blue carbon include reintroducing tidal flow and sediment delivery by altering water regulation structures (e.g., dams), area-based conservation, urban planning/zoning to reduce coastal squeeze, vetting new development using well-researched Environmental Impact Assessments, active restoration, and subsidizing high-carbon species (Kelleway et al., 2020; Lovelock and Reef, 2020). Habitat restoration efforts have shown high plant return and carbon storage; in particular, seagrass transplants are clonal and can therefore proliferate rapidly (Duarte et al., 2013; Orth et al., 2020). Existing blue-carbon restoration is challenged by (1) inability to trade soil-carbon credits due to an absence of scientific data supporting soil-carbon accounting (Siikamaki et al., 2013), (2) loss of seedlings due to altered rainfall/sedimentation and the threat of SLR (Wylie...
et al., 2016), and (3) lack of political frameworks to support blue carbon markets (Kelleway et al., 2020). Additional research is needed to resolve the role of macroalgae in carbon storage, the effects of disturbance on carbon release, and whether calcifying organisms like algae are carbon sources or sinks, among other topics (Macreadie et al., 2019).

6. Conclusion

As the effects of climate change intensify worldwide, there is mounting global momentum to expand protected areas that maximize ecosystem function, carbon capture, and benefits to people (Dinerstein et al., 2020). Ecosystem connectivity is a key variable in this process, as connectivity allows benefits from one ecosystem to cascade across multiple ecoregions. Coastal ecosystems represent areas of intense connectivity, and have been identified as areas that maximize returns in biodiversity from ocean conservation (Zhao et al., 2020). In particular, CMS are some of the most vulnerable land-sea ecosystems, and provide high, synergistic conservation benefits if protected together. We identify locations worldwide where CMS spatially overlap within 1 km. We also outline four conservation efficiencies that arise from jointly managing these ecosystems: (1) increased resistance to threats, as boundary habitats buffer disturbances from land and sea, (2) high biodiversity within small geographic areas, (3) habitat portfolio effects that generate refugia for displaced organisms, and (4) increased economic incentives through mutually supportive ecosystem services.

Several research gaps impede joint conservation in CMS. Importantly, the spatial scale of spillover effects between systems is not well known. In one study, higher coral recruitment due to algae control by herbivores occurred on reefs within 250 m of mangroves, relative to reefs > 500 m from mangroves (Olds et al., 2014). Additional research suggests that mangrove-reef connectivity via mobile organisms can extend up to at least 500 m (Martin et al., 2015). However, uncertainty remains about how the spatial scale of connectivity is affected by factors such as species home ranges, local hydrodynamics, and bathymetry (Olds et al., 2012), and how existing scales of connectivity will shift under climate change. Determining the geographic extent of ecosystem connectivity will be crucial in determining the size and proximity of MPAs and TPAs for joint conservation. In addition, the datasets that we used to analyze global mangrove, seagrass and reef ecosystems, while the best available, have significant omissions and errors. Our ability to delineate these ecosystems is expected to vastly improve in the near future through maps of reef extent from the Allen Coral Atlas (https://allencoralatlas.org/), and additional remote sensing innovations.

Conservation planning is further slowed by sparse examples of intentional, joint MPA-TPAs. While our spatial analysis shows that 18% of the mangrove-seagrass-reef interactions (based on 1-km habitat proximity) are incidentally protected, few conservation areas are explicitly designed to maximize land-sea connectivity (Giakoumi et al., 2019; Harris et al., 2019). As a result, the efficacy of joint land-sea conservation is difficult to directly measure, and many studies rely upon modeling or scenario analysis to forecast the effect of joint conservation (Guannel et al., 2016; Oleson et al., 2018). Future studies may customize these models to mangrove-seagrass-reef interactions, or conduct case studies focused on the joint MPA-TPAs that exist in order to transfer lessons learned to additional coastal areas.

The majority of research on CMS interactions focus on a single direction of impact, from mangrove to reef. Future studies are needed to document the effects of reefs on the diversity and abundance of mangroves, seagrasses, and associated species (e.g., fisheries). For example, how does the disturbance of coral reefs impact seagrasses or mangroves nearby? Does loss of reefs primarily affect specific successional stages of seagrass and mangrove development, i.e., the early establishment of plants, which may benefit most from low-energy environments? Where do specific degradation processes such as coral bleaching result in cascading impacts on neighboring ecosystems? Are TPAs more effective when paired with MPAs in storm-prone areas? Research into these issues can help managers understand the strength and timing of bilateral connectivity, and drive more terrestrial managers to lead land-sea conservation.

Finally, there are numerous research gaps regarding the fundamental ecology of CMS interactions. Benefits of seagrass conservation are understudied, in part because seagrasses are uncharismatic and overlooked as a conservation priority (Duarte et al., 2008; Unsworth et al., 2019). A lack of scientific and public awareness of seagrass benefits to society and global decline pose challenges to prioritizing their conservation (Orth et al., 2006). As noted, seagrasses are often dredged by hotels as a nuisance, and additional public education is necessary to highlight seagrasses benefits to coral reefs and fish populations, i.e., tourist attractions. The global area of seagrasses is highly uncertain, ranging from 300,000 to 600,000 km², due to national biases as well as the difficulty of detecting seagrasses in historical remote sensing datasets, particularly in deep water (Duarte et al., 2013; Macreadie et al., 2019), and therefore monitoring tools for seagrasses are urgently needed. In addition, there are conflicting results regarding the role of mangroves as climate refugia for corals. On the one hand, many species of corals are found growing in association with mangroves (Yates et al., 2014) but on the other hand, the low light and extreme sediment and biochemical conditions of mangroves select for specially adapted corals (Camp et al., 2019). Whether mangrove-inhabiting corals are specialized for mangrove habitats only, or can help supplement larval flow for reefs and assist with coral growth and establishment, will be important to determine. In addition, in some areas like the USVI, mangrove-coral refugia have suffered destruction from hurricanes and additional research is needed on how these ecosystems can jointly recover (Rogers, 2019).

Together, these knowledge gaps suggest a basic roadmap for future studies. Additional research on ecosystem interactions, with specific focus on the scale of connectivity and influence of climate change, can guide future land-sea spatial planning initiatives. For the purpose of this study we considered system interactions on a conservative basis (≤ 1 km). Remote sensing may help determine the distance across which mangroves and reefs reinforce each other’s health and structure, and can further identify human settlements where building ecosystem services (e.g., ecotourism, blue carbon markets, storm protection) may be beneficial. This research, in turn, can assist conservation managers in establishing joint TPA-MPAs, using existing decision-support templates (Tallis et al., 2008) and social-science insights on effective stakeholder engagement (Alvarez-Romero et al., 2011; Jupiter et al., 2017). Ideally, new MPA-TPAs
in the future will fuel case studies that help to refine future interventions and identify new knowledge gaps, cyclically informing land-sea conservation. Finally, research collaboratives across multiple disciplines are necessary to provide timely and coherent information to policymakers across the land-sea divide.

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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