Marine Environmental Research 197 (2024) 106479

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Impact of human disturbance on biogeochemical fluxes in tropical seascapes

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ARTICLE INFO

Keywords:
Biogeochemical fluxes
Disturbance
Ecosystem functioning
Mangrove
Seagrass
Coral reef
Positive interactions

ABSTRACT

Tropical seascapes rely on the feedback relationships among mangrove forests, seagrass meadows, and coral reefs, as they mutually facilitate and enhance each other's functionality. Biogeochemical fluxes link tropical coastal habitats by exchanging material flows and energy through various natural processes that determine the conditions for life and ecosystem functioning. However, little is known about the seascape-scale implications of anthropogenic disruptions to these linkages. Despite the limited number of integrated empirical studies available (with only 11 out of 81 selected studies focusing on the integrated dynamics of mangroves, seagrass, and corals), this review emphasizes the importance of biogeochemical fluxes for ecosystem connectivity in tropical seascapes. It identifies four primary anthropogenic influences that can disturb these fluxes-nutrient enrichment, chemical pollution, microbial pollution, and solid waste accumulation-resulting in eutrophication, increased disease incidence, toxicity, and disruptions to water carbonate chemistry. This review also highlights significant knowledge gaps in our understanding of biogeochemical fluxes and ecosystem responses to perturbations in tropical seascapes. Addressing these knowledge gaps is crucial for developing practical strategies to conserve and manage connected seascapes effectively. Integrated research is needed to shed light on the complex interactions and feedback mechanisms within these ecosystems, providing valuable insights for conservation and management practices.

1. Introduction

1.1. *Tropical seascapes and their habitats*

Tropical seascapes often consist of mangroves, seagrass and coral reefs, with mangrove forests at the land-sea interface. The value of these habitats is frequently expressed by their capacity to provide ecosystem goods and services (de Groot et al., 2012). For example, these habitats play a significant role in nutrient cycling, carbon sequestration, erosion control, coastal protection, acting as nursery ground for marine organisms, and food production (Christianen et al., 2013; Donato et al., 2011; Huxham et al., 2018; Taillardat et al., 2018; Williams et al., 2013). On a global scale, their presence is considered essential for addressing and mitigating climate change due to their disproportionately large contribution to global atmospheric carbon sequestration (IPCC, 2022). Furthermore, the ecological functioning of each of these habitats (e.g., primary production, nutrient cycling, nursery and feeding habitat) is considered higher in connected seascapes due to facilitative interactions. Facilitative interactions refer to positive interactions that improve conditions by alleviating abiotic stress (Gillis et al., 2014; van de Koppel et al., 2015), which will be described in detail in sections 1.3 and 1.4.

1.2. *Threats and consequences of human activities on tropical seascapes*

Mangrove forests, seagrass meadows, and coral reefs are among the most threatened habitats in the world (Polidoro et al., 2010). Their deterioration due to human activities is intense and rapidly expanding (Jouffray et al., 2020). Approximately 35% of mangroves, 50% of coral reefs, and 30% of seagrass have been lost or degraded worldwide in the last fifty years (Bruno et al., 2018; Donato et al., 2011; Hoegh-Guldberg et al., 2017; Orth et al., 2006; Waycott et al., 2009). Human activities along the coasts are driving intensified efforts to meet the growing demand for resources (Jouffray et al., 2020), often without adhering to sustainability standards. These activities include fishing (Shantz et al., 2019), mining (Asir et al., 2020), beach and diving tourism (Giglio et al.,

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https://doi.org/10.1016/j.marenvres.2024.106479
Received 13 December 2023; Received in revised form 20 February 2024; Accepted 25 March 2024

2020), and infrastructure development (Alharbi et al., 2017). Furthermore, climate change with multiple sudden and slow-onset impacts, posses a global threat to tropical seascapes (Ward et al., 2016). While some mangrove forests can adaptively migrate landwards in response to sea level rise, the presence of urban infrastructure in the coastal zone limits their ability to relocate, resulting in coastal squeeze (Gilman et al., 2007). Coastal squeeze and deforestation of mangrove forests may cause a generalised disruption of the interaction network (Gillis et al., 2017a). Similarly, the fragmentation of one connected habitat can trigger cascading degradation effects on the other habitats due to the loss of facilitative effects. For example, fragmentation of seagrass meadows may negatively affect the remaining fraction of the meadow as it disrupts sediment stabilisation patterns (El Allaoui et al., 2016), seed dispersal (Livernois et al., 2017), and organic matter fluxes (Ricart et al., 2015). The degradation of one habitat, such as mangroves, can also impact remaining habitats, e.g., corals, due to the lack of nutrient buffering against the increased flow of nutrients into the water. This disruption alters the balance between corals and macroalgae, leading to higher algal cover (Keyes et al., 2019).

1.3. *Cross-ecosystem connectivity*

Cross-ecosystem interactions between coral reefs, seagrass, and mangroves typically involve shifts in transfers of biomass (Bastos et al., 2022), energy (Odériz et al., 2020), and biogeochemistry (Briand et al., 2015; Camp et al., 2016). Although there are variations in this model, most commonly, a zonation pattern from mangroves to seagrass to corals is formed based on an environmental gradient dictated by the combination of ecological factors (e.g. nutrient tolerance and availability) and hydrological factors (e.g. tidal regimes, wave action, freshwater inputs) in tropical coasts. Cross-ecosystem interactions involving various substances and fluxes (Fig. 1) improve the ecological performance of coral, seagrass and mangrove systems (Earp et al., 2018; Gillis et al., 2014; van de Koppel et al., 2015).

For instance, mangroves trap nutrients from land sources and create a salinity gradient, lowering these pressures on seagrass. Vice versa, seagrass plays a role in erosion control and sediment binding, which results in land accretion and more stable ground for mangroves. At the same time, retain sediment particles and nutrients for the benefit of corals. Corals reefs influence seagrass beds positively by acting as barriers for hydrodynamic forces such as waves and wind. Although connectivity can refer to the movement of any material from one spatial point to another, this article explicitly focuses on biogeochemical connectivity, i.e. biogeochemical fluxes, further explained in section 1.4.

1.4. *Biogeochemical connectivity*

Research on the effects of connectivity in coastal seascapes has been disproportionally focused on biotic and physical interactions, likely due to easier monitoring, leaving biogeochemical fluxes relatively understudied. Biogeochemical fluxes are also included in Fig. 1. Van de Koppel et al. (2015) defined biogeochemical fluxes as “a supply of non-living substances moving from one habitat to another”, making them intrinsic links within the interaction network. In other words, biogeochemical materials move between the three habitats, acting as connections. These fluxes not only occur in one direction, but they form a network. Due to the limited understanding of larger-scale implications and the crucial role that organic matter, nutrients, and various chemical species play in the tropical coastal interaction network, this study focuses on biogeochemical fluxes with and without human disturbance. While a few reviews have discussed the role of facilitative interactions (e.g., Earp et al., 2018), none have explicitly focused on the understudied biogeochemical fluxes involved in cross-ecosystem connectivity in tropical seascapes, such as nutrient removal and pH buffering. Therefore the objectives of this study are 1) to quantify the empirical studies and provide an overview of biogeochemical fluxes affected by anthropogenic pressures and their consequences for cross-ecosystem interactions between mangroves, seagrass, and corals, and 2) to identify knowledge gaps and new research opportunities that arise from anthropogenic disruptions to connected tropical seascapes.

2. Literature review

To provide an overview of biogeochemical fluxes relevant to cross-ecosystem connectivity in tropical seascapes, anthropogenic pressures, and their impacts, a literature search was conducted. The selection of studies was a multi-step process that began by identifying the most relevant terms and concepts (“mangrove”, “seagrass”, “coral”, “tropical”, “connected/connectivity”, “flux”, “export”, “import”), which were combined to create search strings. Alternative search terms that are frequently used synonymously to ecosystem connectivity such as “interaction”, “link(age)”, “long distance effect”, “pathway”, “exchange”, and “cascade” were also considered. During the initial screening phase, several grouping themes were recognised, thus allowing us to refine our search for each of the different fluxes investigated, i. e. carbonate chemistry and pH, solid waste, microbial pollution,

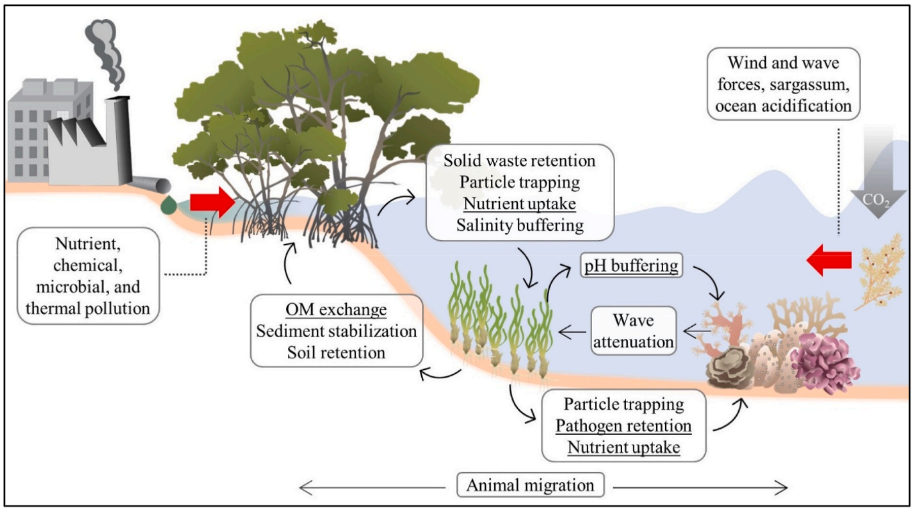

Fig. 1. Synthesizing conceptual scheme showing the interactions known so far in connected seascapes. Human pressure (red arrows) gives rise to a number of drivers that enter and modify the interaction network. Black arrows indicate the source and receptor of the service provided. Biogeochemical fluxes are underlined.

chemical pollution, and carbon stocks and nutrients. This research was performed using Scopus and Google Scholar databases. Articles resulting from the search were then screened, and those empirical studies consisting in the exchange of fluxes between the habitats of interest, or the import/export of biogeochemical material from a single habitat were included. Additional papers included in this study were identified through a subsequent forward search. Therefore, the literature reviewed in this article included, but was not limited to, that resulting from the search strings. A final number of 81 peer-reviewed articles in English were analysed and listed in Table A1. The literature searches were concluded in June 2023, prior to the submission of this article for publication. Consequently, studies published after this date are not included.

Articles selected for review were categorized by habitat, type of fluxes studied, and year of publication. Those articles that included the study of several types of fluxes were cross-classified (i.e. classified within more than one category). We provide a state of knowledge about biogeochemical fluxes in tropical seascapes (section 3), as well as the dominant anthropogenic drivers of change and their impacts (section 4). These anthropogenic drivers were not targeted by the literature review, but they were identified from the selected studies. Lastly, novel research pathways are identified (section 5).

3. Results and discussion of main findings

We found that research interest in biogeochemical fluxes in tropical seascapes has been relatively low, but it has exponentially increased over the last decade. In 2019 alone, there were a total of 13 studies and the number has gradually decreased until the present time (Fig. 2A). However, out of the 81 articles reviewed, only 11 included all three habitats of interest, namely mangroves, seagrass and corals (Fig. 2B). According to the literature sources reviewed, mangroves are the most frequently studied habitat among the three in relation to biogeochemical fluxes, followed by seagrass and corals. However, studies focused on more than one habitat are significantly lacking (Fig. 2B). The varying frequency with which different types of biogeochemical fluxes appear in the selected articles shows clear differences, suggesting that certain fluxes may not have receive the same level of attention as others. In particular, the selected literature provides limited coverage of the role of mangroves and seagrass in pathogen removal (Fig. 2C, “microbial pollution”). On the other hand, organic carbon and nutrient fluxes have received the most frequent attention, closely followed by studies on carbonate chemistry and pH, as well as chemical pollution (Fig. 2C).

Examining the geographic distribution of selected studies reveals a notable focus in the Caribbean, with the Indo-Pacific region and (south) Asia also showing a high concentration of selected studies. While the selected studies cover ecosystems across the globe, research in Australia, Africa, South America, and the Middle East is comparatively less prevalent.

From our literature survey, it becomes evident that empirical studies that include all three components of the tropical seascape, i.e., mangroves, seagrass, and corals are still scarce. Similarly, studies focusing on any combination of two habitats are also limited (Fig. 2B). Out of 11 “integrated” studies identified, 5 were related to carbonate chemistry and pH across the seascape, 5 studies focused on carbon stocks and nutrients, and 1 study included both types of fluxes. A comprehensive overview of the complete literature survey can be found in Table A1.

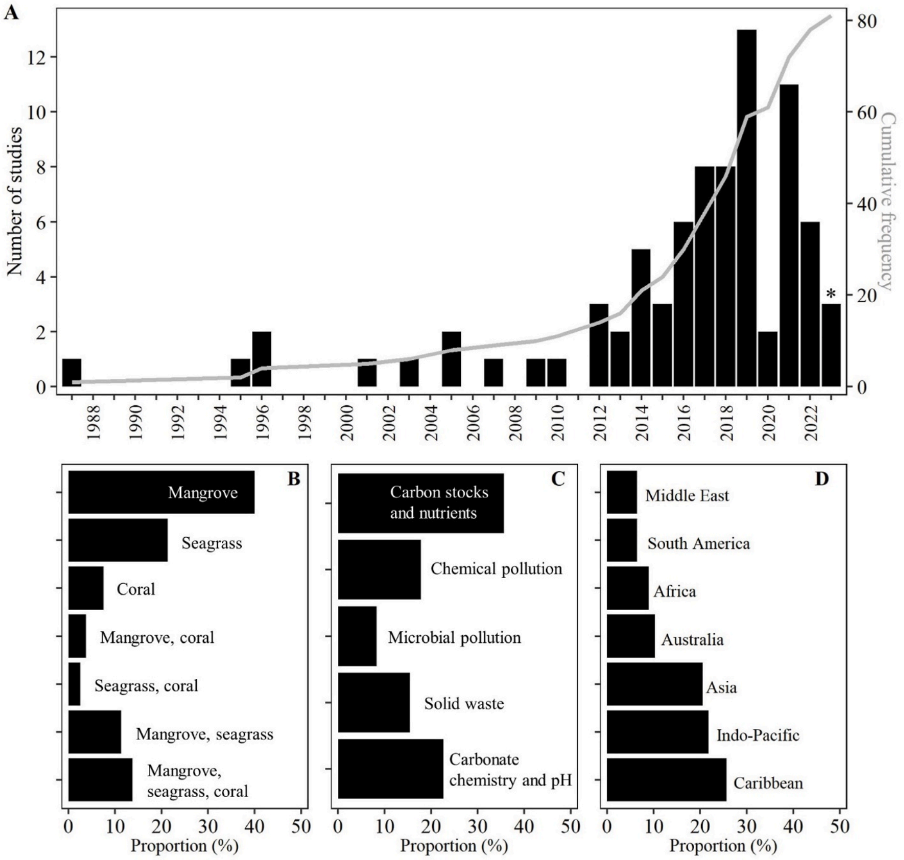

Fig. 2. Number of studies included in this review classified by (A) year of publication from 1987 up until 2023*, (B) habitat of study, (C) type of fluxes investigated, and (D) geographic distribution. *Studies selected for 2023 extend only until June, encompassing publications from the first six months of the year.

4. Anthropogenic pressures that impact biogeochemical fluxes

Despite the scarcity of integrated studies, we have conducted a review of the available literature on biogeochemical fluxes and the connectivity between mangroves, seagrass and coral reefs, both in natural state and under anthropogenic disruption. In the following sections, we describe and discuss the impacts of four major anthropogenic drivers that we have identified in our literature review (Table A1). These drivers are nutrient enrichment (section 4.1), chemical pollution (section 4.2), microbial contamination (section 4.3), and solid waste accumulation (section 4.4). Although microbes are living entities and do not fit within the definition of "biogeochemical fluxes" (as outlined in section 1.4), they are included in this review (section 4.3) as their occurrence is governed by biogeochemical dynamics. Additionally, microplastics, a product of the degradation and a major component of solid waste, pose significant threats to tropical seascapes, including toxicity, accumulation, disease transmission, and mechanical injuries. While solid waste itself is not a biogeochemical flux, it is an anthropogenic driver whose presence affects biogeochemical fluxes, and thus it is included in section 4.4 of this review.

4.1. Nutrient enrichment

In the tropical seascape, mangrove, seagrass and coral reefs thrive by maintaining a tight balance of nutrients. Both mangroves and seagrasses act as nutrient filters, removing a considerable fraction of the nutrient load (Evrard et al., 2005; Moroyoqui-Rojo et al., 2015; Sandoval-Gil et al., 2016; Stapel et al., 1996; Stapel et al., 2001), potentially preventing excess nutrients from reaching the coral reef and seagrass from the land-side (Gillis et al., 2016; Keyes et al., 2019). Mangrove forests, located at the land-sea interface, receive and uptake nutrients and organic matter of terrestrial sources (Adame et al., 2012; Agraz-Hernández et al., 2018) although these inputs often buffered by terrestrial ecosystems (Williams et al., 2013). Therefore, their spatial co-occurrence can form a protective cascade against coastal eutrophication (Gillis et al., 2014). As the organic matter load from mangroves is context and site-dependent (Signa et al., 2017), they may serve as subsidiaries of organic matter and nutrients to seagrass and corals (Adame et al., 2012; Briand et al., 2015; Mishra et al., 2023; Sullivan et al., 2021), while the input of seagrass material also supports mangrove production (Walton et al., 2014). Furthermore, a study on a connected mangrove-seagrass system concluded that higher sediment nutrient concentrations benefit seagrass density and coverage, and consequently their carbon accumulation potential (Kammann et al., 2022). On the other hand, high phosphorus concentrations in soil can decrease mangrove root complexity (as phosphorus is readily available), which negatively affects carbon storage (Kammann et al., 2022). Therefore, the critical nutrient load in connected seascapes not only influences the health and productivity of individual habitats but also the carbon storage potential of the biome.

Anthropogenic disruptions to nutrient connectivity between tropical coastal habitats occur through the introduction of excess nutrients into the system. From the land side, the most common sources of anthropogenic nutrient enrichment are urban wastewater and agricultural effluents (Jones et al., 2018). These agricultural fertilizers and manure flow into the sea due to physical factors like precipitation, leaching, and river transport. Other anthropogenic impacts such as mangrove deforestation cause the mobilization and flow of large nutrient and organic matter loads that were previously retained by mangroves (Asplund et al., 2021; Dahl et al., 2022). Continuous exposure to nutrient enrichment significantly reduces the resilience of mangroves to physical disturbances as observed by Feller et al. (2015), who noted a slower recovery rates of trees after the impacts of a hurricane in areas previously subjected to anthropogenic nutrient loading, as abnormal growth made them more vulnerable to wind damage. As the ecological performance of mangroves declines due to nutrient enrichment, they lose their capacity to filter excess nutrients, allowing more nutrients from land to reach seagrass and corals. Under eutrophic conditions, seagrasses and corals lose their competitive advantage against micro and macroalgae (D'Angelo and Wiedenmann, 2014; Evrard et al., 2005; Govers et al., 2014) which thrive on these nutrients and reproduce rapidly. Seagrasses commonly suffer from overgrowth by epiphytes, resulting in shading and death of the plants (Apostolaki et al., 2012). Similarly, these algae may outcompete corals for light resources and lead to their decline (D'Angelo and Wiedenmann, 2014).

From the sea side, organic carbon and nutrients can also be imported by seaweed (Hidayah et al., 2022), or in the form of sargassum brown tides resulting from large-scale anthropogenic enrichment of continental rivers and offshore areas (Djakouré et al., 2017). This phenomenon, which began in 2011 and has occurred yearly since then, involves the influx of sargassum algae to Caribbean and West African coasts (Oyesiku and Egunyomi, 2014; Sissini et al., 2019; Van Tussenbroek et al., 2017). The nutrients imported by sargassum brown tides are released into the water column as the algae wash up on the shore begin to decompose (Van Tussenbroek et al., 2017). Algae decomposition leads to high nutrient turnover rates, thereby exacerbating the eutrophication effects. In addition to the large amounts of nutrients imported by sargassum, its decomposition also results in the accumulation of sulphide and ammonium in sediments and water, causing toxicity to animals (Rodríguez-Martínez et al., 2019) and plants such as mangroves (Hernández et al., 2022), seagrass, and corals (Van Tussenbroek et al., 2017). Mangrove basins and channels are particularly prone to sargassum accumulation (Hernández et al., 2022; León-Pérez et al., 2023) possibly due to being trapped in their complex mangrove root systems. The broader implications of sargassum brown tides for connected seascapes are not yet fully understood, nor is the natural capacity of mangroves, seagrass and corals acting in association to counteract their impacts.

4.2. Chemical pollution

Chemical pollution in coastal areas originates from various human activities, including agriculture (Duke et al., 2005; Santos et al., 2019), industrial water discharge (Shete et al., 2009; Vaiphasa et al., 2007), and solid waste disposal (Garcés-Ordóñez et al., 2019). High concentrations of heavy metals in coastal areas are often associated with the presence of industrial activities (Ngole-Jeme et al., 2016). The ability of mangroves to act as biofilters and retain pollutants in their sediments has been extensively studied (e.g. Chai et al., 2019; Shi et al., 2019). Mangroves can also uptake and translocate these pollutants within their tissues, leading to their bioaccumulation (Analuddin et al., 2017; Arumugam et al., 2018; Dudani et al., 2017). Moreover, seagrasses have the capacity to absorb heavy metals and can be used for phytoremediation in polluted water bodies, although their exposure to these substances severely impacts their health (Yadav et al., 2021), and that of grazers by bioaccumulation (Wilkinson et al., 2022).

Pesticides and herbicides are also common pollutants present in mangrove sediments (Bhattacharya et al., 2003) and they have been linked to massive mangrove dieback events (Duke et al., 2005). In sub-lethal concentrations, pesticides can be taken up by mangroves and bioaccumulated in leaf and other tissues (Shete et al., 2009). Moreover, maritime traffic and offshore activities increase the risk of oil spills, and the fuels can be absorbed by mangrove roots, causing tree mortality within a few days of exposure (Teas et al., 1987). A 29-year-long study on the effects of oil pollution on a mangrove-seagrass-coral continuum revealed significant long-term damage and slow recovery of mangroves, whereas no dramatic impacts on seagrass were observed, and corals were documented to fully recover after ten years (Renegar et al., 2022). Other experimental exposures of mangrove pods to oil have proven to be toxic and detrimental to their early development (Proffitt et al., 1995). Thus, a knowledge gap remains concerning the multifaceted impacts of chemical pollution on tropical seascapes including bioaccumulation, pesticides, oil spills, and ecosystem recovery.

4.3. Microbial pollution

Due to structural and chemical mechanisms, mangroves and seagrasses provide several protective services to corals, such as buffering sediment outflows and trapping suspended particles (Christianen et al., 2013; Keyes et al., 2019). These mechanisms enable tropical coastal habitats to reduce exposure to microbial contamination, including pathogenic bacteria (Lamb et al., 2017) and antibiotic-resistant bacteria (Zhao et al., 2019), while also acting as sinks for chemical pollution (Analuddin et al., 2017) thus protecting the overall biome. The main sources of microbial pollution are municipal wastewater discharge and aquaculture activities (Lamb et al., 2017; Liu et al., 2023).

A study by Lamb et al. (2017) demonstrated that the incidence of coral disease caused by sewage-derived bacterial pathogens in the vicinity of seagrass meadows was 50% lower compared to reefs without adjacent seagrass. Tall and dense seagrass meadows are more effective at capturing bacterial pathogens by retaining particles compared to fragmented seagrass meadows (Liu et al., 2023). The specific mechanism by which seagrass remove pathogens from the trapped particles is not fully understood, but Deng et al. (2021) suggested that seagrass segregates anti-bacterial phytochemicals as a stress response to anthropogenic pressure. An increased abundance of microbial pathogens in tropical coasts, in combination with other stressors such as eutrophication (section 4.1), could potentially lead to a higher incidence of infectious diseases in seagrass meadows (Hughes et al., 2018; Sullivan et al., 2018) and seagrass-associated species (Liu et al., 2018). Furthermore, mangrove sediments have been proven to remove antibiotic-resistant bacteria from sewage effluents (Zhao et al., 2019), and compost inoculated with mangrove-associated fungi reduces plant disease incidence (Ameen and Al-Homaidan, 2021). Thus, mangroves and seagrass can mitigate microbial contamination, particularly from sewage-derived pathogens. However, the specific mechanisms remain incompletely understood, highlighting a need for further research.

4.4. Solid waste

Marine plastic pollution is a globally concerning issue that poses a serious threat to marine ecosystems. Plastic items have been found in high densities in some of the world's largest connected seascapes (Wilson and Verlis, 2017). While plastics can be retained for long periods (Ivar do Sul et al., 2014), their persistence depends on plant density and topography (Cordeiro and Costa, 2010). In a Colombian mangrove lagoon, the highest concentrations of microplastics were found near populated areas (Garcés-Ordóñez et al., 2019), highlighting that improper waste disposal is a source of plastics in the tropical seascape.

Furthermore, the study by Wilson and Verlis (2017) identifies tourism as the primary cause of marine plastic debris in the Great Barrier Reef, with areas closest to tourism infrastructure being the most polluted. The complex 3D structure and intricate root systems of mangroves play a key role in retaining and trapping solid debris from land and ocean-based sources (Cordeiro and Costa, 2010). Some negative effects of these accumulations include the clogging of tidal channels (Fig. 3A), which increases salinity in the lagoons (Bulow and Ferdinand, 2013) and suffocates the trees by covering their aerial roots (van Bijsterveldt et al., 2021). According to Martin et al. (2020) mangroves are experiencing an exponential increase of plastic burial in their sediments. Over time, retained plastic items degrade into microplastics while remaining trapped and accumulating within the vegetation (Li et al., 2018). Furthermore, mangroves have been found to retain marine microplastics with their leaves through adsorption and adhesion, acting as a coastal microplastic sink (Li et al., 2022). A recent study found that seagrass meadows can influence water flow and depositional dynamics, favouring the accumulation of plastics in their sediment (Unsworth et al., 2021), which could hinder their free movement (Fig. 3B).

Further out at sea, corals, with their filter and suspension feeding capacity, are highly exposed to marine microplastics. Numerous coral species have been shown to remove microplastics from the water column through ingestion (Hankins et al., 2018; Rotjan et al., 2019) and adhesion to the surface of these particles (Corona et al., 2020). The presence of large amounts of floating plastic could potentially reduce the photosynthesis of coral symbionts and negatively impact colony health by depriving them of light (Osinga et al., 2008). Additionally, the study by Lamb et al. (2018) concluded that the probability of corals experiencing infectious diseases is 20 times higher when they come into contact with plastics (Fig. 3C). Plastics cause mechanical damage and abrasion to coral tissue, creating entry points for pathogens. These authors also found that corals ingest microplastics colonized by microbes, which can lead to disease. Lamb et al. (2018) estimated that approximately 11.1 billion plastic items (diameter >50 mm) are polluting the Asia-Pacific coral reefs, and these number is expected to increase by 40% in 2025.

This exponential increase in plastics and microplastics in mangrove, seagrass, and coral habitats affects and degrades all three components of the seascape. It directly impacts each habitat individually, hampering their natural functions and, consequently, disrupting cross-ecosystem connectivity. However, limited knowledge exists regarding the larger-scale resilience of the connected seascapes to solid waste pollution, and to (micro) plastics in particular.

4.5. pH and carbonate unbalance

According to recent studies, there is ongoing debate regarding the potential influence of seagrasses and mangroves on seawater pH adjacent to coral reefs, especially regarding mangroves.

The extent to which seagrasses can effectively remove CO2 and have a significant positive effect on water pH depends on factors such as their photosynthetic efficiency, which is influenced by light availability and intensity (Ow et al., 2016), as well as water temperature and salinity (George and Lugendo, 2022). Diel variations in light, resulting in fluctuations between day and night, lead to variations in the net primary productivity of seagrass. This productivity is not only directly relates to their pH buffering capacity but is also influenced by the local hydrodynamic conditions (Barry et al., 2013). Model-based (Unsworth et al., 2012), field (Ricart et al., 2021), and laboratory experiments (Bergstrom et al., 2019; George and Lugendo, 2022) have confirmed the significant contribution of seagrasses to increasing water pH (Fig. 4), potentially benefiting adjacent reef-forming species. Unsworth et al. (2012) applied a theoretical approach using data from several publicly available sources to examine seagrass productivity and estimated that seagrass could enhance coral calcification by up to 18% due to localized increase in water pH. On the other hand, the modelling approach of Koweek et al. (2018) concluded that seagrass could only temporarily increase water pH, suggesting that they could not provide a long-term solution. However, Bergstrom et al. (2019) conducted an ex-situ experiment and found that calcification rates of reef species in the presence of the seagrass *Halodule wrightii* were approximately twice as high as in its absence, and Ricart et al. (2021) observed that seagrass ameliorated low pH in 65 % of the sampled locations.

An integrative study conducted by Camp et al. (2016) examined mangrove, seagrass and coral reef ecosystems at three different sites in the Pacific, Indian and Atlantic. The study confirmed the pH buffering capacity of seagrass, as they increased the mean water pH, supporting coral calcification in the adjacent reef. Similarly, a recent study in a connected tropical seascape in the western Indian Ocean found that seagrass ecosystems considerably raised water pH and potentially mitigated low pH in adjacent mangrove and coral ecosystems (George and Lugendo, 2022). The mean pH in mangrove areas was consistently lower than that in seagrass and coral reef sampling points (Camp et al., 2016; George and Lugendo, 2022). Biogeochemical processes occurring in mangrove areas such as plant and microbial respiration, and organic matter mineralization, contributed to increased levels of CO_2. While mangroves may not act as a buffer for ocean acidification in coexisting mangrove-coral habitats, the generally lower pH levels (Stewart et al.,

Fig. 3. Mangroves retain plastics that would otherwise be transported by rivers to the sea. A) Plastic waste accumulation in Sungai Klang mangrove basin, Malaysia and covering of aerial roots (Aldrie Amir, 2018). B) Seagrass meadow littered with plastic.[11] C) Plastic bag wrapped around coral (Bourzac, 2018).

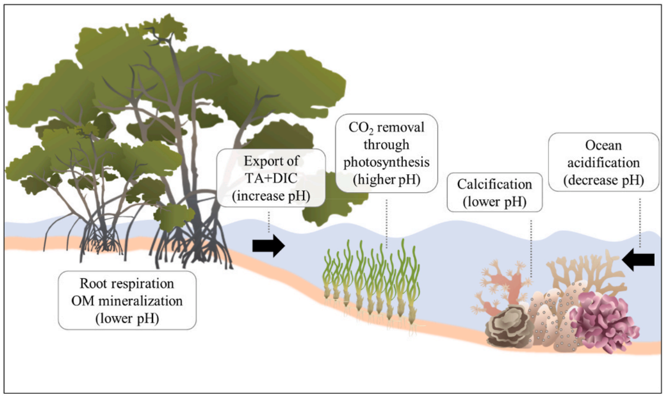

Fig. 4. Conceptual model showing the potential contribution of tropical coastal habitats to water pH regulation. TA: total alkalinity. DIC: dissolved inorganic carbon. OA: ocean acidification.

2022) could pre-condition adjacent corals to future acidic waters (Camp et al., 2016, 2019; Yates et al., 2014). This evidence emphasizes the importance of maintaining healthy seagrass meadows as a buffer zone between mangroves and corals. A more recent empirical study on the capacity of connected mangroves, seagrasses, and corals as sources or sinks of CO_2 indicated that mangroves and corals (to a lesser extent) acted as sources, while seagrasses played an uptake role (Macklin et al., 2019). According to Chen et al. (2021), mangroves globally export an estimated 83 ± 50 Tg C yr^{-1} of dissolved CO_2 to the open ocean, which is a larger amount of carbon than they sequester in sediment. On the other hand, an integrated study by Akhand et al. (2021), showed that the mangroves in a mangrove-seagrass-coral continuum acted as net sources of total alkalinity. Furthermore, a study of six different locations along the Australian coast by Sippo et al. (2016) demonstrated that mangroves exported DIC and alkalinity to adjacent waters (Fig. 4) thus creating a buffer against ocean acidification.

Water pH and alkalinity exhibit high variability within seasons, days, and even hours due to tidal variation, temperature, light intensity, and local hydrodynamic conditions, as well as biotic factors (Cyronak et al., 2018; Saderne et al., 2019). Salma et al. (2022) found no significant differences in water pH between mangrove-dominated sites, seagrass-dominated sites, and sites where mangroves and seagrass co-occur. Consequently, the results regarding the relative contribution of cross-ecosystem connectivity to ocean acidification buffering are often contradictory and highly dependent on local conditions. It remains uncertain whether these habitats can buffer ocean acidification to benefit coral calcification or, conversely, precondition corals to higher stress levels, potentially losing this service due to anthropogenically-induced pH imbalances. When excess nutrients enter the system, decomposition rates, microbial activity, and sulfate production increase, leading to acidification (Middelburg et al., 1996). Therefore, a key knowledge gap exists regarding the extent to which nutrient enrichment of tropical coastal habitats may create a pH unbalance that disrupts the existing alkalinity/acidity fluxes.

5. Impacted systems give way for potential new research pathways

Following the identification of knowledge gaps in section 4, we highlight what we consider the main research questions that need to be addressed regarding biogeochemical connectivity in tropical seascapes.

- Can the interactions between tropical habitats mitigate the effects of eutrophication and sulphide accumulation from sargassum brown tides?
- Does the retention of sargassum by mangrove roots increase the exposure of adjacent seagrass and coral habitats, intensifying its impact to the biome?
- Can mangroves reduce bacterial loads in seawater through litter fall and export to adjacent seagrass and coral habitats, thus reducing disease incidence?
- Can connected mangrove-seagrass systems serve as refugia for sensitive organisms against ocean acidification or alleviate low pH in the benefit of adjacent coral reefs?
- Can bioaccumulated contaminants in mangrove leaves be transferred to adjacent habitats through litter fall and export?
- Does plastic waste entanglement in mangrove roots and microplastic retention in seagrass sediment restrict the free movement of (micro) plastics within the biome?

Mechanistic understandings of processes driving the potential pH buffering by mangroves or the capacity of their leaf phytochemicals to reduce pathogen load can be obtained through relatively simple mesocosm experiments. Other simple techniques, such as chlorophyll fluorescence, can be utilized for regular monitoring of mangrove, seagrass and coral health, serving as an indicator of stress caused by human pressure in tropical seascapes. These experiments may also provide us with answers to significant remaining questions, such as the ones described in sections 5.2 and 5.3. Furthermore, citizen science may aid in documenting and assessing changes in tropical seascapes affected by sargassum (section 5.1). These data, combined with the application of remote sensing techniques that can assess the quality of large or remote seascapes from aerial or satellite images, could enhance data availability and contribute to our understanding of whether these habitats can individually or collectively counteract the effects of sargassum. In the sections below (5.1–5.3), we elaborate on some of these questions and provide suggestions on how to best apply this knowledge.

5.1. *Resistance to brown tides*

The spatial co-occurrence of mangroves, seagrasses, and corals might also play a vital bioremediation role when it comes to sargassum brown tides. The accumulation and decomposition of sargassum lead to eutrophication, dissolved oxygen depletion, and toxic levels of sulphide and ammonium, causing the loss of flora and fauna (Rodríguez-Martínez et al., 2019; Van Tussenbroek et al., 2017). The impacts of sargassum accumulation and toxicity to coastal habitats have been documented in recent years (Hernández et al., 2022; León-Pérez et al., 2023; Rodríguez-Martínez et al., 2019) but the capacity of ecosystem connectivity to dampen subsequent eutrophication and sulphide toxicity is yet to be determined. Furthermore, floating sargassum masses obstruct incoming sunlight, while the decomposition of organic matter consumes dissolved oxygen, leading to the formation of anoxic zones on the seafloor (Van Tussenbroek et al., 2017). The resulting reduction in light and excessive algal growth have a negative impact on numerous marine organisms, particularly seagrass and coral. However, the interactive effects of shading, oxygen depletion, and other factors remain to be empirically tested. A recent review highlights the potential of the three connected systems to mitigate the effects of hypoxia through their interactions and self-rescue mechanisms (Altieri et al., 2021). According to these authors, the photosynthetic production, storage, absorption and redistribution of oxygen within their tissues can counteract hypoxia in their environment. Furthermore, mangroves and seagrasses are well-known natural biofilters (Agraz-Hernández et al., 2018; Sandoval-Gil et al., 2016). It could be hypothesized that these habitats, acting in association, could more rapidly dampen other impacts of sargassum than each individual habitat in isolation, and positively influence their recovery after disturbance (Gillis et al., 2014) thus preventing the decline of the entire biome. On the other hand, mangrove root systems are prone to sargassum accumulation due to their spatial complexity, leading to mangrove decline (Hernández et al., 2022; León-Pérez et al., 2023). It could also be hypothesized that the accumulation of sargassum in mangrove root systems increases the exposure time of neighbouring seagrass and corals to toxic compounds, leading to the collapse of the biome. We identify three important future research directions: 1) empirically testing the interactive effects of multiple sargassum-related impacts on the health of affected habitats, 2) determining the relative contribution of connected mangroves, seagrass and corals in mitigating the impacts of sargassum, compared to their contributions in isolation, and 3) understanding the negative effect of sargassum retention by mangroves on the connected seascape.

5.2. Reduction of bacterial pathogens

Like seagrass, mangroves might have the ability to protect adjacent systems from bacterial pathogens (Ameen and Al-Homaidan, 2021; Zhao et al., 2019). Mangrove tissues contain a wide range of phytochemicals with biocidal properties. Preparations of mangrove bark, root and leaf material have been used for centuries in traditional medicine to cure infections (Bandaranayake, 1998) and are now a novel source of antimicrobial compounds widely used by the pharmaceutical industry.

Phytochemical screenings indicate that mangrove leaves are particularly rich in secondary metabolites, such as steroids, triterpenes, saponins, flavonoids alkaloids, tannins, and phenolic compounds (Amaral-Zettler et al., 2015; Eswaraiah et al., 2020; Santhi and Sengottuvel, 2016; Shi et al., 2010). These phytochemicals can naturally leach from mangrove leaves after only a few hours in seawater (Fig. 5). Up to 23% of mature leaf dry mass can consist of these bioactive phytochemicals (Kandil et al., 2004). When chemically extracted from mangrove leaves, phytochemical compounds exhibit strong antimicrobial activity against various human, animal, and plant pathogens (Bandaranayake, 1998; Eswaraiah et al., 2020; Manilal et al., 2009; Mishra and Sree, 2007; Prabhakaran et al., 2012). However, is it yet to be determined whether untreated, raw mangrove leaves have a comparable effect to their laboratory-created extracts in inhibiting the growth of bacteria. It could be hypothesized that large amounts of mangrove litter regularly fall from the trees and are subsequently exported to adjacent systems due to local hydrodynamic conditions, thus releasing their phytochemicals elsewhere, for instance at the nearby seagrass meadows and coral reefs (Fig. 5).

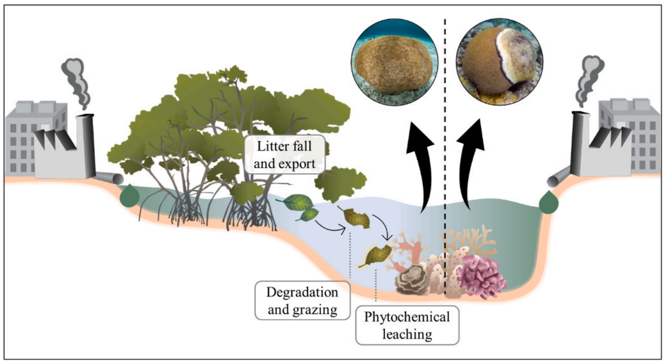

Fig. 5. Conceptual model showing the hypothetical fate of mangrove phytochemicals and their potential antimicrobial service to coral reefs. Healthy brain coral in connected seascape on the left (Photo credit: Oceana), and coral suffering from black band disease in seascape without mangroves on the right (Photo credit: Wikipedia).

If this is the case, mangroves may act as cleansing agents, particularly in areas where adjacent habitats are affected by diseases related to pathogens due to the absence of well-functioning urban sanitation systems. Therefore, research priorities include understanding how naturally extracted mangrove phytochemicals influence microbial pathogen abundance and whether, in combination with adjacent seagrass meadows, they function as protective cascades against microbial pathogens for the benefit of coral reefs.

While direct empirical evidence is currently lacking, a synthesis of several studies suggests that coral microbial activity holds the potential to positively influence adjacent habitats such as mangroves and seagrass by providing nutrients and combating pathogenic presence. Schiller and Herndl (1989) observed that the interstitial spaces within corals, where microbial activity is high, can serve as a source of nutrients for other organisms. Additionally, Koh (1997) showed that corals are capable of chemically inhibiting microbial colonization. A study by Shnit-Orland and Kushmaro (2009) demonstrated that bacteria associated with coral mucus, an integral part of the coral microbiome, produce antimicrobial substances, protecting the coral from infections. Ritchie (2006) supported this understanding by showing how coral mucus can regulate microbial populations, thus potentially influencing the microbial community in the surrounding coral reef environment. Although the direct relationship between coral microbial activity and the protection of adjacent habitats is not empirically tested, it is conceivable that these antimicrobial functions of corals could extend to nearby mangroves and seagrass, potentially serving as a defense against pathogenic diseases, which remains as an open question.

5.3. Ocean acidification refugia

Lastly, the capacity of mangroves and seagrasses to act as refugia for coral reefs against ocean acidification, as shown in Fig. 4, still carries some uncertainty due to conflicting evidence discussed in section 4.5, particularly regarding the role of mangroves (Camp et al., 2016; George and Lugendo, 2022; Macklin et al., 2019; Ricart et al., 2021; Saderne et al., 2019; Sippo et al., 2016). Although many of these discrepancies may be attributed to the local environmental conditions where the studies were conducted and the mangrove species under investigation, a key priority is to determine the extent to which tropical seascapes that include mangroves and seagrass can serve as refugia for coral reefs in the

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[1] https://a-z-animals.com/blog/the-importance-of-seagrass-beds-and-the-animals-youll-see-there/.

face of ocean acidification. If confirmed, the close proximity to seagrass and mangroves as potential long-term shelters could be considered in the decision-making process for future coral reef restoration programs.

6. Conclusions

This review explores the complex dynamics of biogeochemical fluxes and habitat connectivity in tropical seascapes formed by mangroves, seagrass, and coral reefs, shedding light on both natural processes and anthropogenic disruptions. Our results show the impacts of four major anthropogenic drivers i.e., nutrient enrichment, chemical pollution, microbial pollution, and solid waste accumulation, on the transfer of energy, nutrients, and biomass between connected habitats in tropical seascapes. These disruptions manifest as eutrophication, increased disease incidence, toxicity, and disturbances in water carbonate chemistry.

Moreover, we highlight the emerging issue of sargassum blooms, emphasizing the need for further research to understand their effects on biogeochemical processes and habitat connectivity. Despite the challenges posed by anthropogenic disturbances, our review identifies venues for future research. These include studying the transfer of phytochemicals with antibacterial properties, as well as bioaccumulated contaminants through mangrove litter fall and export to adjacent habitats. We also propose exploring the potential for the biome to sequester (micro)plastics or restrict their movement, as well as the prospect of mangroves and seagrass acting in association to increase local water pH to counteract the threat of ocean acidification on coral reefs. While some of these venues for future research are further discussed and solutions to advance our understanding are proposed, other remain as open questions. By addressing these critical gaps in knowledge we can improve our understanding of biogeochemical connectivity in tropical seascapes and develop effective strategies to mitigate the impacts of anthropogenic disruptions on mangroves, seagrass, and corals. Future conservation and restoration efforts in tropical seascapes need to consider cross-ecosystem connectivity and address any topic biases in their approach. It is crucial to gather robust empirical evidence that can effectively guide conservation practices in relation to cross-ecosystem connectivity.

CRediT authorship contribution statement

Sara P. Cobacho: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ingrid A. van de Leemput:** Writing – review & editing, Supervision, Conceptualization. **Milena Holmgren:** Writing – review & editing, Supervision, Conceptualization. **Marjolijn J.A. Christianen:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interest

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.

Data availability

Data will be made available on request.

Acknowledgements

This work was carried out under the Netherlands Earth System Science Centre (NESSC) program. This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 847504. It has been further financially supported by the Dutch Ministry of Education, Culture and Science (OCW). We appreciate the valuable reviews by Prof. Dr. Marten Scheffer and Dr. Ir. Miquel Lürling, which have helped to improve the quality of the manuscript. We acknowledge the Media Centre at the University of Maryland as the source of the vector images utilized in creating the figures for this paper, significantly enhancing the clarity and quality of our visual representations.

Appendix

Table A 1
Summary overview of empirical studies on biogeochemical fluxes in tropical seascapes included in the literature survey.

Fluxes	Habitats of study	References
Carbon stocks and nutrients	Mangrove, seagrass, coral	(Adame et al., 2012; Briand et al., 2015; Hernández et al., 2022; León-Pérez et al., 2023; Middelburg et al., 1996; Signa et al., 2017)
	Mangrove, seagrass	(Asplund et al., 2021; Dahl et al., 2022; Hidayah et al., 2022; Kammann et al., 2022; Mishra et al., 2023; Sullivan et al., 2021; Walton et al., 2014)
	Mangrove, coral	Keyes et al. (2019)
	Mangrove	(Agraz-Hernández et al., 2018; Analuddin et al., 2021; Feller et al., 2015; Gillis et al., 2016; Moroyoqui-Rojo et al., 2015; Vaiphasa et al., 2007; Williams et al., 2013)
	Seagrass	(Apostolaki et al., 2012; Evrard et al., 2005; Govers et al., 2014; Liu et al., 2018; Stapel et al., 1996, 2001; Van Tussenbroek et al., 2017)
	Coral	D'Angelo and Wiedenmann (2014)
	Other (macroalgae, bacterial communities, etc)	(Djakouré et al., 2017; Liu et al., 2018)
Chemical pollution	Mangrove	(Analuddin et al., 2017; Arumugam et al., 2018; Bhattacharya et al., 2003; Chai et al., 2019; Dudani et al., 2017; Duke et al., 2005; Ngole-Jeme et al., 2016; Proffitt et al., 1995; Qiu et al., 2019; Santos et al., 2019; Shete et al., 2009; Shi et al., 2019; Teas et al., 1987)
	Seagrass	(Fonseca et al., 2017; Yadav et al., 2021)
Microbial pollution	Mangrove	(Ameen and Al-Homaidan, 2021; Zhao et al., 2019)
	Seagrass	(Deng et al., 2021; Liu et al., 2023)
	Coral	Lamb et al. (2018)
	Seagrass, coral	Lamb et al. (2017)
	Seagrass, bacterial communities	Liu et al. (2018)
Solid waste	Mangrove	(Cordeiro and Costa, 2010; Garcés-Ordóñez et al., 2019; Ivar do Sul et al., 2014; Li et al., 2022; Martin et al., 2019, 2020; van Bijsterveldt et al., 2021; Wilson and Verlis, 2017)
	Coral	(Corona et al., 2020; Hankins et al., 2018; Lamb et al., 2018; Rotjan et al., 2019)
	Others (beach ecosystem, bacterial communities, etc)	(Li et al., 2018; Wilson and Verlis, 2017)

(continued on next page)

Table A 1 (*continued*)

Fluxes	Habitats of study	References
Carbonate chemistry and pH	Mangrove, seagrass, coral	(Akhand et al., 2021; Camp et al., 2016; George and Lugendo, 2022; Macklin et al., 2019; Middelburg et al., 1996; Saderne et al., 2019)
	Mangrove, seagrass	(Salma et al., 2022; Sandoval-Gil et al., 2016)
	Mangrove, coral	(Camp et al., 2019; Yates et al., 2014)
	Seagrass, coral	Unsworth et al. (2012)
	Mangrove	(Chen et al., 2021; Sippo et al., 2016)
	Seagrass	(Barry et al., 2013; Bergstrom et al., 2019; Cyronak et al., 2018; Koweek et al., 2018; Ow et al., 2016; Ricart et al., 2021)

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