Exploring feedback mechanisms for nitrogen and organic carbon cycling in tropical coastal zones

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The anthropogenic introduction of significant amounts of reactive nitrogen in the coastal zone particularly since the discovery and application of the Haber-Bosch process has profound consequences over organic carbon storage and transformations at both regional and global scales. Here, we review our current knowledge on cause-effect chains for nitrogen, especially dissolved inorganic nitrogen, on organic carbon cycling in coastal tropical systems. We focus on the feedback mechanisms for turnover of different organic carbon species to nitrogen excess and links to current environmental and climate changes. We pay special attention to organic carbon dynamics in tropical coasts due to their high primary productivity, rapid sedimentation, and significant needs of nitrogen for agriculture and industry usages. Together with land-use changes and economy development, we highlight the vulnerability of carbon storage in tropical coasts triggered by nitrogen overloading and outline possible industrial strategies with low carbon cycling disturbance to benefit the development of tropical countries.

Introduction

Coastal belts are zones of intense organic carbon storage and cycling due to the close interaction between the land, the sea, the benthic compartment and the atmosphere. Enhanced local productivity adds to the transport of terrestrially-derived organic material through surface loading or submarine groundwater discharge (Bianchi et al., 2018; Jiang et al., 2020). As the electron donor (energy provider) in heterotrophic biogeochemical reactions, the importance of organic carbon on element cycling is fundamental. Similarly, nitrogen is an essential element for life and frequently

enriched in coastal zones due to its vast and intensive application in agriculture and industry (Hutchins and Capone, 2022). Nitrogen is particularly mobile in the biosphere due to its large range of chemical forms and redox states, participating in a wide range of biogeochemical reactions. Both the quantity and quality of organic carbon are important drivers of benthic heterotrophic nitrogen reaction pathways (Ibánhez and Rocha, 2017), which in turn control the abundance and composition of benthic microbiota or pelagic plankton species (Rocha et al., 2022). Moreover, the autotrophic reactions in nitrogen cycling, e.g., nitrification, are also tightly linked to carbon sources since the labile fraction of organic carbon (e.g., amino acids and polypeptide) is essential in benthic metabolism (Castaldelli et al., 2019). The high primary production characteristic of coastal zones compared to the open ocean together with carbon transport from the continent lead to high standing stocks of organic carbon. In tropical coastal systems, a significant fraction of this carbon is preserved in different compartments such as mangroves, seagrass meadows, macroalgae forests and phytoplankton, with different retention time scales (Spivak et al., 2019). The high sequestration rates in the tropical zone accumulate substantial quantities of organic carbon, in layers even reaching several meters in thickness (e.g., peat) along coastal lines (Wu et al., 2019). Despite the importance of the tropical coastal organic carbon pool in the global carbon cycle, the feedback mechanisms between organic carbon and dissolved inorganic nitrogen (DIN) are barely explored though a tight reaction chain between carbon and nitrogen exists. Here, we review organic carbon storage and cycling patterns and reactive linkages between DIN and organic carbon in tropical coastal zones. In addition, the economic dimension of these processes is discussed, with a focus on industry development targeting reduced carbon emissions and national economy development of tropical countries.

Organic carbon cycling in tropical coasts

The high temperature and intense precipitation characteristic of tropical shores (frequently > 2000 mm yr^{-1}) accelerate the hydraulic cycle and hence favor the transport of terrestrial organic carbon (both dissolved: DOC and particulate: POC) across the land-ocean interface (Moore et al., 2013; Figure 1A). Additionally, large forest coverage in river catchments enhances terrestrial carbon content in river water. Rivers flowing through tropical peatland contain substantial humic materials and the DOC concentration in tea-color river waters can reach >2000 µM even in small river catchments (e.g., Maludam River, Malaysia; river catchment of 432 km^2; Martin et al., 2018). Even in tropical rivers without peat coverage (e.g.,

Wenchang River, China), the riverine DOC level still ranges from 150 to 560 µM (Fu et al., 2013), frequently higher than similar rivers located in sub-tropical and temperate zones, e.g., Changjiang (108 to 133 µM, Bao et al., 2015), Rhine River (240 µM) and Thames River (298 µM; Painter et al., 2018). Highly turbid rivers (e.g., Rajang, Malaysia) are also major contributors of land-derived POC to the tropical coast (Zhu et al., 2020). This tropical riverine carbon transport gains disproportionate importance during tropical storms and erosive transport of POC to the coast (Hilton et al., 2008). Tropical rivers are estimated to account for about ~60% of the global continental carbon transport to the coast (Ludwig et al., 1996). The acceleration of the hydrologic cycle also increases the transport of organic carbon through submarine groundwater discharge (SGD), of particular importance in tropical islands (Moosdorf et al., 2015). The continental endmember of SGD is frequently enriched in high-molecular DOC species derived from plant tissue decomposition and hence SGD is a non-point source of complex DOC to tropical coasts (Wu et al., 2021).

The volatile fractions of DOC would evaporate from land into the atmosphere and reach coastal zones *via* dry and wet deposition (Chow et al., 2010). Atmospheric transport can be also a relevant source of POC to the tropical coast, particularly during fire events as black carbon (Liu et al., 2022) and aeolian dust, particularly in the tropical Atlantic originated from the Sahara and the Sahel (Eglinton et al., 2002; Ibánhez et al., 2022). The high temperature of tropical zones further enhances coastal ventilation and terrestrial volatile compounds are rapidly spread through Walker Circulation to long distances from the source (Jiang et al., 2021a). The *in-situ* production of DOC and POC in tropical coastal ecosystems mainly due to the activity of different primary producers is also a large source of organic carbon due to the general high productivity of tropical coasts (Figure 1A). Decay and decomposition of this primary production and resulting debris feeds the coastal and benthic organic carbon inventory.

Before setting on the seabed, a fraction of DOC and POC, typically labile fractions (L-DOC), e.g., oligosaccharides and amino acids, is rapidly consumed in coastal waters by a wide range of microbiota-mediated reactions (Nelson and Wear, 2014). Generally, the residence time of highly labile DOC in ocean waters is up to approximately one week (Hopkinson et al., 2002). The fate of this reactive DOC pool includes adsorption onto mineral substances, biological assimilation and fully consumption to carbon dioxide (CO_2). Organic matter mineralization generally increases with increasing temperature and thus, it is particularly intense in tropical coastal ecosystems (Cardoso et al., 2014). The recalcitrant DOC fraction dispersed in coastal waters, such as humic materials, presents residence times that can reach years to decades (Opsahl and Benner, 1997). Apart from exportation to the adjacent open ocean, persistent organic matter fractions are buried in coastal sediments *via* diagenesis, undergoing benthic aerobic (surface 2 to 10 cm
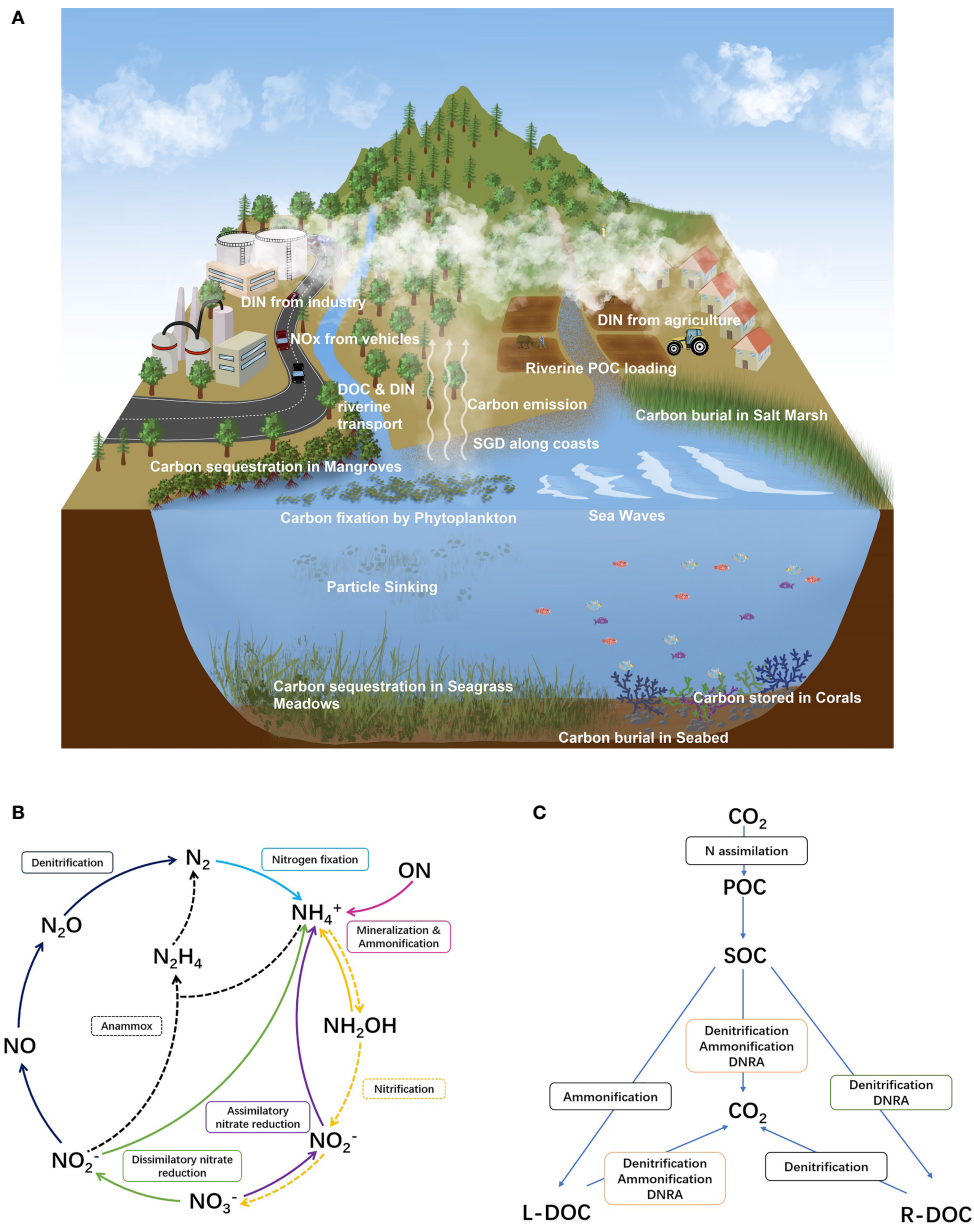
FIGURE 1

Sketch of carbon storage and transport routes in coastal zones **(A)**. This figure also shows the main transport routes of terrestrial DIN to the coast; **(B)** Biogeochemical cycling of N in marine environments with different pathways. ON indicates organic nitrogen. In the figure, reactions with dash lines indicate autotrophic reactions while the solid indicates heterotrophic reactions; **(C)** transformation among SOC, labile DOC (L-DOC), recalcitrant DOC (R-DOC), POC and CO_2 in sediment environments coupled with different N reaction pathways (including priming effects).

depth) and anaerobic (frequently below 10 cm depth) transformations (Bianchi et al., 2018). Currently, the global flux of carbon from land to coastal oceans is assumed to be 616 Tg yr^{-1}, of which approximately 210 Tg yr^{-1} is retained in coastal sediments (Barrón and Duarte, 2015). Tropical mangroves alone are responsible for ca. 26 Tg yr^{-1} of organic carbon burial, i.e., about 12% of the global burial rate of global coastal sediments (Breithaupt et al., 2012).

Biogeochemical feedbacks of nitrogen to carbon cycling

Coastal zones also receive substantial reactive nitrogen, mainly derived from a series of anthropogenic activities, such as agriculture, sewage disposal, petrochemical industry, fermentation engineering, etc. (Jiang et al., 2019). The geographical overlap between DIN and organic carbon

enrichment in coastal zones defines the tightly biogeochemical interaction of these elements. According to the compartment, the influence of DIN on carbon cycling and storage in tropical coastal zones is summarized as:

Benthic environments: In cohesive sediments, the effects of DIN additions on carbon storage vary significantly under aerobic and anaerobic conditions. In aerobic layers, mainly the top layer (from a few mm to 1-2 cm), nitrate (NO_3^-) and nitrite (NO_2^-) compete with a series of strong oxidants, especially dissolved oxygen (DO) and ferric iron (Song et al., 2021). In this environment, NH_4^+ production *via* mineralization and ammonification requires the supply of organic matter, indicating carbon consumption (Figure 1B). Due to the relatively weak oxidation potential compared to dissolved oxygen, NO_3^- and NO_2^- may participate in benthic carbon cycling *via* stimulating microbial growth and adding POC in both oxic and anoxic sediments (Figure 1C). The importance of NO_3^- and NO_2^- as oxidants gains relevance in anoxic sediments due to the oxidation of organic carbon (production of CO_2) *via* the denitrification process (Figure 1C). Heterotrophic denitrification may include the oxidation of both DOC and sediment organic carbon (SOC) in sediment columns (Plummer et al., 2015, Figure 1C), Even the degradation of recalcitrant organic pollutants in mangrove sediments could be accelerated by the presence of NO_3^- likely *via* carbon-dependent denitrification (Jiang et al., 2016). Similarly, organic carbon, especially labile fractions, such as phytoplankton debris, is also needed for the dissimilatory nitrate reduction to ammonium (DNRA) process in coastal cohesive sediments (Hardison et al., 2015). The presence of other low-molecular organic compounds, such as oxalate, citrate and glucose, could also markedly enhance DNRA rates (Liu et al., 2016). In fact, DNRA rates showed higher sensitivity to labile carbon additions than denitrification (Robinson et al., 2018). Heterotrophic denitrification and DNRA compete for electron donors from variable carbon sources in benthic systems (Figure 1C). Although the fermentative DNRA process is still poorly understood, highly reducing and organic rich conditions, high NO_3^- and high C to N ratios in the organic matter all seem to favor DRNA over canonical denitrification (Fazzolari et al., 1998; Tomaszek and Rokosz, 2007). As such, DNRA seems to be a dominant nitrate reduction process in tropical cohesive sediments (Dong et al., 2011). Although both heterotrophic processes produce the potent greenhouse gas N_2O as byproduct, the potential prevalence of DNRA over denitrification has strong implications for C and N cycling in coastal tropical ecosystems: the end-product of DNRA is ammonium, thus recirculating N into bioavailable forms, eventually reaching surface waters where it can feed the N_2O-producing nitrification process and enhance primary production. Another anoxic, microbially-mediated DIN process is the autotrophic Anammox (anaerobic ammonium oxidation), that reduces nitrite with ammonium to produce N_2.

Notably, anammox doesn't produce N_2O as byproduct (Van De Graaf et al., 1996). In cohesive marine sediments, anammox shows a negative correlation with the labile organic carbon content (Rich et al., 2020). In permeable sediments, DO penetration depths that can be orders of magnitude higher than in cohesive sediments, favoring the creation of anoxic microniches thus placing oxic and anoxic DIN processing in close proximity (e.g., Jiang et al., 2021b). The injection of NO_3^- into permeable sediment porewaters has been identified to enhance denitrification rates, although porewater DOC content, even the labile fractions, seems not to be the preferred carbon source when SOC is present (e.g., Jiang et al., 2018a; Jiang et al., 2021b). DNRA in permeable sediments also significantly relays on carbon sources. More importantly, DNRA could have stronger carbon mobilization potential than denitrification due to a higher relative proportion in NO_3^- removal in permeable sediments compared to cohesive sediments as found in the northern Baltic Sea (Hellemann et al., 2020). The high organic matter breakdown capacity of permeable sediments prevents the accumulation of large quantities of organic matter. These organic carbon-poor conditions could favor the occurrence of the autotrophic anammox process by limiting heterotrophic nitrate reduction pathways as observed in temperate latitudes (e.g., Kroeger and Charette, 2008). Adding to the commonly found organic C limitation of the local microbial community, N seems to be also in deficit in these environments. In temperate permeable sediments, the sudden availability of DIN within the porewater seems to act as a "primer" of SOC decomposition by precluding N limitation of the local community and increasing their ability to process refractory SOC (Ibánhez and Rocha, 2014; Ibánhez et al., 2021). Consequently, DIN addition accelerates SOC processing, limiting the ability of permeable sediments to store organic C. Despite the low sedimentary organic carbon content characteristic of coastal permeable sediments, their large volume suggests this may be an important mechanism of organic C mobilization. Whether this effect occurs in tropical permeable sediments is yet to be confirmed.

Water column: DIN amendment enhances OC storage in primary producers, while the assimilation of NO_3^- likely consumes DOC in cells (Figure 1B). N fixation function also requires OC from phytoplankton cells while such losses could rapidly be compensated by photosynthesis. DIN additions to coastal water can trigger desorption of DOC from suspended particle surfaces due to competition with sorption sites (Engel and Chefetz, 2016). In surface waters, DOC and POC are significantly influenced by photo-reactions, such as photobleaching, particularly intense in the tropical zone (Zhou et al., 2019). The breakdown of high-molecular carbon compounds produces labile organic matter fractions for the transformation of DIN *via* aerobic denitrification, typically occurring on particle surfaces (Jiang et al., 2019) and hence

accelerates the consumption of organic carbon by heterotrophs. Moreover, apart from toxicity effects derived mainly from the addition of NH_4^+ (toxicity varied among species; Collos and Harrison, 2014), DIN additions could significantly enhance the biomass of primary producers in coastal waters and hence increase biological POC and DOC pools promoting large ecological changes (e.g., proliferation of harmful algae blooms), eutrophication and oxygen decline (e.g., Peyman et al., 2017). Eutrophication may provide water column low-oxygen (micro)environments favoring the occurrence of denitrification, anammox and DNRA in surface waters (Broman et al., 2021). As an heterotrophic process, denitrification decreases the organic carbon pool while denitrifiers in anoxic water may preferentially utilize fresher and labile autochthonous POC instead of DOC (Zeng et al., 2019). DNRA in hypoxic waters also prefers autochthonous carbon (Broman et al., 2021), while the preference between POC and DOC is still undocumented. In the tropical zone, together with high water temperatures, the loading of exogenous nutrients may easily boost the carbon pool in waters, while the organic carbon enrichment then accelerates decomposition *via* heterotrophic pathways. Compared with denitrification, DNRA still stores reactive nitrogen in the DIN inventory. Linked with nitrification, DNRA continuously consumes pelagic organic carbon and produces N_2O. Anoxic C processing enhancement together with accelerated N cycling drove by eutrophication seems to enhance greenhouse gas production (CO_2, CH_4 and N_2O) in tropical estuaries (Nguyen et al., 2022).

Atmosphere: Atmospheric transport is a key fertilization process to support surface ocean carbon fixation (Ibánhez et al., 2022). In addition, aerosols are also a pool for organic carbon, containing substance from terrestrial volatilization (Jiang et al., 2021b) and emission of sea spray driven by waves (Rinaldi et al., 2020). Organic fractions could be attached on the surface of colloidal particles, while the residence time is still limited due to the exposure to ultraviolet rays, varying from several hours to weeks. The main interaction between DIN species and organic carbon in the atmosphere is mainly *via* different photochemical reactions in aerosols. In particular, the decomposition of organic matter in aerosols near the ocean surface likely produces substantial small molecular acids, such as oxalic acid and formic acid (Carlton et al., 2007). NH_4^+ in aerosols tends to neutralize these acid compounds. The effect of nitrogen oxides would be more complex. NO_3^- in the humid atmosphere could produce OH^- and $O(^3P)$ after receiving ultraviolet rays. A similar production of OH^- is also obtained when NO_2 and NO are exposed to strong sunlight. Both OH^- and $O(^3P)$ have a great oxidation capability, accelerating the decomposition of organic carbon in aerosols (Dominé and Shepson, 2002). Currently, though research on the chemical dynamics related with organic carbon and DIN in the tropical atmospheric environment is limited, the strong sunlight exposure and high

temperature likely accelerates the organic carbon decomposition and leads to lower DOC content of wet deposition.

Biota: Anthropogenic DIN enhances the growth of primary producers and increases carbon sequestration but also eutrophication and other deleterious effects over the coastal biota (Howarth, 1988). In tropical ecosystems, apart from phytoplankton and algae living in the water column, mangrove forests and seagrass meadows contribute substantially to carbon fixation. Nevertheless, seagrass meadows are very sensitive to increasing DIN loads. For instance, DIN enrichment decreases eelgrass shoot density and biomass (Deegan et al., 2002). Anthropogenic DIN additions to tropical seagrass ecosystems can promote toxicity to the individuals and large ecological changes such as the growth of epiphytes and algae with direct impacts over seagrass populations (Burkholder et al., 2007). In contrast, the amendment of NO_3^- and NH_4^+ to the surrounding water column of mangrove forests could stimulate their growth even when the loading level could be toxic to phytoplankton species. Mangrove ecosystems generally buffer the transfer of redundant N originated from land to the coast while stimulating their growth (Wu et al., 2008). This growth stimulation promoted by DIN addition varies among leaves, roots and stems. Incubation experiments showed that the addition of NH_4NO_3 to mangrove sediments follows the roots>leaves>stems route (Jiang et al., 2016). Compared with stems and leaves, carbon retention rates associated to roots in sediments is higher due to lower impacts of hydraulic transport. This reinforces the significance of mangrove systems in carbon sequestration along tropical coasts. Apart from direct influence on root biomass, DIN amendment also conditions the interaction between plant roots and sediments in the rhizosphere (Jiang et al., 2016). The addition of DIN can significantly stimulate root activity (Jiang et al., 2018b), thus enhancing the release of low-molecular sugar and amino acids (Weng et al., 2013). More importantly, mineralization of SOC in the rhizosphere seems not accelerated by DIN additions (Keuskamp et al., 2013). Overall, the organic carbon pool in the rhizosphere might be enhanced by increasing DIN loadings originated from land, reinforcing the large contribution of mangrove forests to the global blue carbon pool. Nevertheless, the long-term impact of N enrichment over the stored C pool of mangrove ecosystems remains uncertain. Along coasts, coral reefs (warm water species) are exclusive of tropical ecosystems and N additions promote large impacts over them and related carbon processing (Lønborg et al., 2018). Generally, coral reefs are flourished in oligotrophic environments with a rapid internal nutrient circling *via* decomposition and nitrogen fixation to sustain their growth (O'Neil and Capone, 2008). Low-level NH_4^+ likely enhance coral growth rate, while NO_3^- addition increases oxidative stress in corals (Zhao et al., 2021). The amendment of excess DIN to coral reefs enhances the incidence of coral diseases caused by predation on corals (Zhao et al., 2021) and hence

decreases the organic carbon pool in coral systems. More importantly, eutrophication driven by DIN additions to coral reefs likely increases algal bloom frequencies and invasion of macro algae (Lapointe et al., 2019), leading to a permanent change in organic carbon storage and carbon cycling in these regions.

Economic evaluation and development

The enhanced production of greenhouse gases due to anthropogenic disturbance of tropical ecosystems promotes profound negative feedbacks in the climate system and the biosphere. To prevent further degradation, the emission of greenhouse gases to the atmosphere has been regulated in a series of global conventions. Consequently, carbon sequestration represents now economic income from a market trading while greenhouse gas emissions likely result in economic losses (Ellerman et al., 2008). Organic carbon storage and mobilization in tropical coasts is highly dynamic and strongly linked to DIN cycling. Accordingly, increased N inputs likely influence the local economy. For instance, high levels of NO_3^- in tropical waters trigger CO_2 emissions *via* heterotrophic pathways (Figure 1C). To completely reduce 10 µM of riverine NO_3^-, approximately equal levels of SOC/DOC need to be transformed to CO_2 in coastal environments. In a low discharge tropical river (e.g., the Indus River, Pakistan, 5 km^3 yr^{-1}), such CO_2 emission can lead to an economic loss of around 51, 000 Euro each year based on recent costs in the European Climate Exchange (around 85 Euro ton^{-1} CO_2 emission during 2022). In average discharge rivers (e.g., Rajang, Malaysia, 110 km^3 yr^{-1}), the annual economic losses to reduce 10 µM of riverine NO_3^- increases to ~1.2 million Euro. Logically, in tropical rivers with large discharges (e.g., Amazon River) or NO_3^- heavily enriched conditions, such economic losses would be much more significant.

Accordingly, proper management on N loading is urgent to tropical countries, both from an environmental and economic point of view. Currently, one of the most significant sources of anthropogenic DIN loads to tropical coasts is the indiscriminate use of fertilizers, which drives the leakage of both NH_4^+ and NO_3^- into the coastal region coupled with hydraulic transport (Table 1). The amount of chemical fertilizer applied in tropical countries is one of the largest globally, such as 415 kg $hectare^{-1}$ yr^{-1} in Vietnam, 569 kg $hectare^{-1}$ yr^{-1} in Egypt and 2106 kg $hectare^{-1}$ yr^{-1} in Malaysia (https://data.worldbank.org/indicator/AG.CON.FERT.ZS). Together with high precipitation rates, the unconsumed fertilizer may directly drain from estuaries and subterranean estuaries into tropical coasts (Lønborg et al., 2021), which highlights the urgency and necessity of a better dimensioning of fertilizer application and replacement from chemical fertilizer to organic fertilizer and slow-release fertilizer thus reducing application quantities (Liang et al., 2022). Moreover, the potentiation of nitrogen-fixing legume species, e.g., Soybean, Groundnut and Cowpea (Peoples and Herridge, 1990), in the tropical agriculture, could favor a balanced N application on land. DIN originated from untreated sewage, i.e., a large pathway for NH_4^+ discharge to the coast, including both municipal and industry, is a global threat to coastal ecosystems particularly near tropical megacities (e.g., Eisenberg et al., 2016). The improvement of the water sanitation network, the installation of highly-efficient treatments in industries combined with small-scale treatments in rural areas would significantly reduce anthropogenic DIN loads to the tropical coast. As another significant contributor of NO_3^- to coastal systems, vehicles based on fuel combustion would necessarily transit towards a different model based on cleaner energy to reduce both greenhouse gas and anthropogenic N emissions. Notably, these schemes and management actions require financial support. In that regard, the economic compensations from improving carbon sequestration in coasts could act as an economic positive feedback mechanism in tropical countries.

From a view of long-term development, a proper industry improvement in the tropical countries would be needed to guarantee the resilience of the stored coastal carbon. Target on the traditional industries, such as agriculture, the replacement of heavily fertilizer-dependent species would be the selection, which requires a sharp understanding on the global market requirement. In addition, the development of eco-tourism in tropical coasts could be further encouraged by

TABLE 1 Anthropogenic Nitrogen sources and potential approaches to reduce DIN emissions to tropical coastal environments.

Sources	Dominant DIN Species	Scale	Influences	Potential improvements
Chemical Fertilizer	NH_4^+ & NO_3^-	Regional	High	Organic fertilizer and slow-release fertilizer replacement, optimization of application
Municipal Sewage	NH_4^+	Point source	High	Treatment improvement, technological advance
Industry Sewage	NH_4^+	Point source	Medium	Regulation improvement
Vehicle Exhausts	NO_3^-	Regional	High	Energy replacement, railway transport
Garbage leak	NH_4^+ & NO_3^-	Point source	Medium	Enhanced regulation and recycling
Graziery Waste	NH_4^+	Point source	Low	Industrial recycling, use as fertilizer

local governments taking advantage of investments from the World Bank, IMF and international travel corporations. The combination of environmentally friendly marine culture and recovery of tropical primary production systems, such as mangrove forests and seagrass meadows, could also enhance carbon income from the global market from long-term trading.

Conclusion

Tropical coastal ecosystems are a key node for global carbon storage, while the organic carbon inventories in many subsystems are significantly influenced by a wide range of biogeochemical factors. This study reviewed the impact of different DIN species (NH_4^+, NO_3^- and NO_2^-) on organic carbon storage in sediments, water column, atmosphere and biological organisms of the tropical band. Generally, apart from stimulation on primary producers, the amendment of NO_3^- and NO_2^- significantly enhances consumption of SOC and DOC, especially labile fractions in sediments and waters *via* heterotrophic reactions. Currently, chemical fertilizer, sewage and vehicle exhaust are key contributors to the DIN pool of tropical coasts, while the management and regulation to constrain DIN outputs require significant economic support. Based on global trading on carbon storage, the financial benefits of carbon sequestration along tropical coasts could act in support of a changing paradigm of tropical coastal uses and resilience.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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