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Nutrient cycling in tropical and temperate coastal waters: Is latitude making a difference?

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ABSTRACT

Tropical coastal waters are highly dynamic and amongst the most biogeochemically active zones in the ocean. This review compares nitrogen (N) and phosphorus (P) cycles in temperate and tropical coastal waters. We review the literature to identify major similarities and differences between these two regions, specifically with regards to the impact of environmental factors (temperature, sunlight), riverine inputs, groundwater, lateral fluxes, atmospheric deposition, nitrogen fixation, organic nutrient cycling, primary production, respiration, sedimentary burial, denitrification and anammox. Overall, there are some similarities but also key differences in nutrient cycling, with differences relating mainly to temperature, sunlight, and precipitation amounts and patterns. We conclude that due to the differences in biogeochemical processes, we cannot directly apply cause and effect relationships and models from temperate systems in tropical coastal waters. Our review also highlights the considerable gaps in knowledge of the biogeochemical processes of tropical coastal waters compared with temperate systems. Given the ecological and societal importance of tropical coastal waters, we hope that highlighting the differences and similarities to temperate systems as well as the existing gaps, will inspire further studies on their biogeochemical processes. Such knowledge will be essential to better understand and forecast impacts on tropical coastal nutrient cycling at local, regional, and global scales.

1. Introduction

Coastal waters cover around 7% of the total ocean surface (26×10^6 km²) while contributing more than 50% of the economic value of the ocean's total ecosystem services (Costanza et al., 2014; Jahnke, 2010). They are the most biogeochemically active zones of the ocean, having

the highest per area nitrogen (N) and phosphorus (P) standing stocks, process rates and transport fluxes (influx and efflux) (Gattuso et al., 1998). Due to this flow of N and P, coastal waters are responsible for 18–33% of the oceanic primary production, 27–50% of the export production (Chen, 2003; Walsh, 1991; Wollast, 1998), 83% of the benthic mineralisation, and 87% of the organic matter burial (Dunne et al., 2007; Middelburg et al., 1993). The processing of N and P is therefore

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enhanced in coastal waters by about two orders of magnitude compared to the open ocean.

Abbreviation list

C	Carbon
CaCO ₃	Calcium carbonate
CDOM	Coloured dissolved organic matter
CFA	Calcium fluorapatite
DOC	Dissolved organic carbon
DON	Dissolved organic nitrogen
DOP	Dissolved organic phosphorus
DIN	Dissolved inorganic nitrogen
DNRA	Dissimilatory nitrate reduction to ammonium
DSi	Dissolved reactive silicon
N	Nitrogen
N ₂	Dinitrogen
N ₂ O	Nitrous oxide
P	Phosphorus
PN	Particulate nitrogen
PP	Particulate phosphorus
Si	Silicon
SGD	Submarine groundwater discharge
SRP	Soluble reactive phosphorus

The impact of human activity on nutrient cycles in temperate zones has been relatively well investigated. Research shows that since the beginning of the 20th Century, the quantity, concentration and relative form (organic versus inorganic) of N and P entering temperate coastal waters from rivers and the atmosphere has been altered (Cloern, 2001; Galloway et al., 2004). These increased N and P fluxes have primarily been linked to intensifying agricultural and livestock production, discharge of sewage and industrial waste, and fossil fuel burning (Galloway et al., 2004), as well as the removal of ecosystem filtering and buffering capacity (e.g. wetland loss) (Verhoeven et al., 2006). While similar changes are likely taking place in tropical coastal waters, nutrient cycling and impacts of human disturbance are less well understood.

Tropical waters generally are considered nutrient poor and therefore should have lower productivity. But tropical coastal waters are productive zones due to permanently higher temperatures and sunlight, with phytoplankton production rates in some cases being comparable to the most productive ocean regions (i.e. upwelling areas) (Nittrouer et al., 1995). In freshwater systems, these higher temperatures and sunlight levels can lead to more intense nutrient cycling at tropical latitudes (Boulton et al., 2008); but whether this is a generalized behaviour for all aquatic systems still needs to be resolved. Human impacts on nutrient cycling in the tropics are also increasing, particularly in Southeast Asia (Halpern et al., 2019). Projections suggest that climate change-driven increases in precipitation, alongside intensifying human activities will lead to substantially increased N loads into coastal waters in South and Southeast Asia by the end of the 21st Century (Sinha et al., 2019). Understanding similarities and differences in nutrient cycling between temperate and tropical coastal waters will help to resolve how human disturbance impacts might differ between climatic zones.

In this manuscript, we compare major components of the two key nutrient cycles (N and P) in temperate and tropical coastal waters. The intent is not to complete an exhaustive review of biogeochemical cycles, but rather to identify critical commonalities and differences in major nutrient cycling pathways. These two broad climatic zones were chosen as temperate coastal waters are relatively well studied, while tropical

waters are some of the least understood coastal systems. We do not include information here on specific anthropogenic sources (e.g. sewage) and sinks (e.g. fisheries) that might be regionally important, but attempt to broadly discuss coastal biogeochemical cycles. We focus on N and P, but other elements (dissolved silicon (DSi) and carbon (C)) are discussed where appropriate to emphasise relevant differences. Identifying how biogeochemical processes of tropical coastal waters differ from temperate areas may further highlight that information from temperate zones is not necessarily applicable to tropical systems and could, if transferred to these systems, lead to incorrect conclusions. Also, approaches used in temperate zones to monitor coastal waters may not be valid in the tropics, and caution is needed when outcomes from temperate systems guide research questions and management approaches in coastal waters worldwide. One example of this is that ecological models based on biogeochemical parameters and process data obtained in temperate regions in some instances are used by managers for understanding e.g. anthropogenic impacts in tropical coastal waters. However, as the biogeochemical cycles are not always comparable, caution is needed before applying these models in tropical settings.

In the following sections we first describe the major environmental difference between tropical and temperate systems (Section 2) followed by a discussion of major nutrient inputs (Section 3.1 Riverine Inputs, 3.2. Groundwater inputs, 3.3 Lateral nutrient fluxes, 3.4. Atmospheric deposition, 3.5. Nitrogen fixation) and recycling (Section 4.1. Cycling of organic nutrients, 4.2. Primary production and respiration, 4.3. Sedimentary nutrient burial, 4.4. Denitrification and Anammox) pathways. Finally, we end with concluding remarks and some future perspectives.

2. Major environmental differences between tropical and temperate systems

Latitudinal gradients are a fundamental feature of the Earth's climate, but definitions of how the tropics are delineated depend on context and may vary between scientific disciplines. In this paper, we take the simplest definition of the tropics as located between the tropics of Cancer (latitude 23°26'North) and Capricorn (latitude 23°26'South), while temperate regions are those with latitudes from 35° to 50° North and South. It is important to recognize that within the tropics, multiple different climatic zones and patterns of seasonality are found, e.g. ranging from permanently higher precipitation especially in equatorial locations to highly seasonal precipitation in other regions, and in some cases monsoon climates. However, a very consistent difference between tropical and temperate systems is seen in temperature and sunlight. The following paragraphs examine how these fundamental environmental variables influence nutrient biogeochemistry in tropical and temperate regions.

Tropical regions receive more solar radiation than higher latitudes, and temperatures are therefore higher and have relatively lower variability. In tropical coastal waters, sea surface temperatures generally range between 20 and 32°C (Fig. 1). In contrast, temperate coastal waters have a more extensive range between 0 and 25°C and a larger seasonal amplitude than tropical regions (Fig. 1). This does not mean that seasonal changes are not evident in tropical coastal waters, but they are not predominantly temperature-driven (Eyre and Balls, 1999). From a biogeochemical point of view, more relevant seasonal changes include dry and rainy seasons causing changes in terrestrial runoff, seasonal shifts in ocean circulation patterns and upwelling events, which can result in changes in water source (river versus marine), nutrient concentrations, and nutrient flux (Davis et al., 2003; Ohowa et al., 1997; Rivera-Monroy et al., 1995; Twilley, 1985).

Some studies suggest that microbial processes are already operating close to their temperature optima in tropical coastal waters, unlike temperate systems, while others propose that tropical marine microbes continue to increase their cycling rates with increasing temperature (Lønborg et al., 2019; McKinnon et al., 2017; Morán et al., 2017; Wiebe and Pomeroy, 1999). Elevated temperatures in tropical waters have

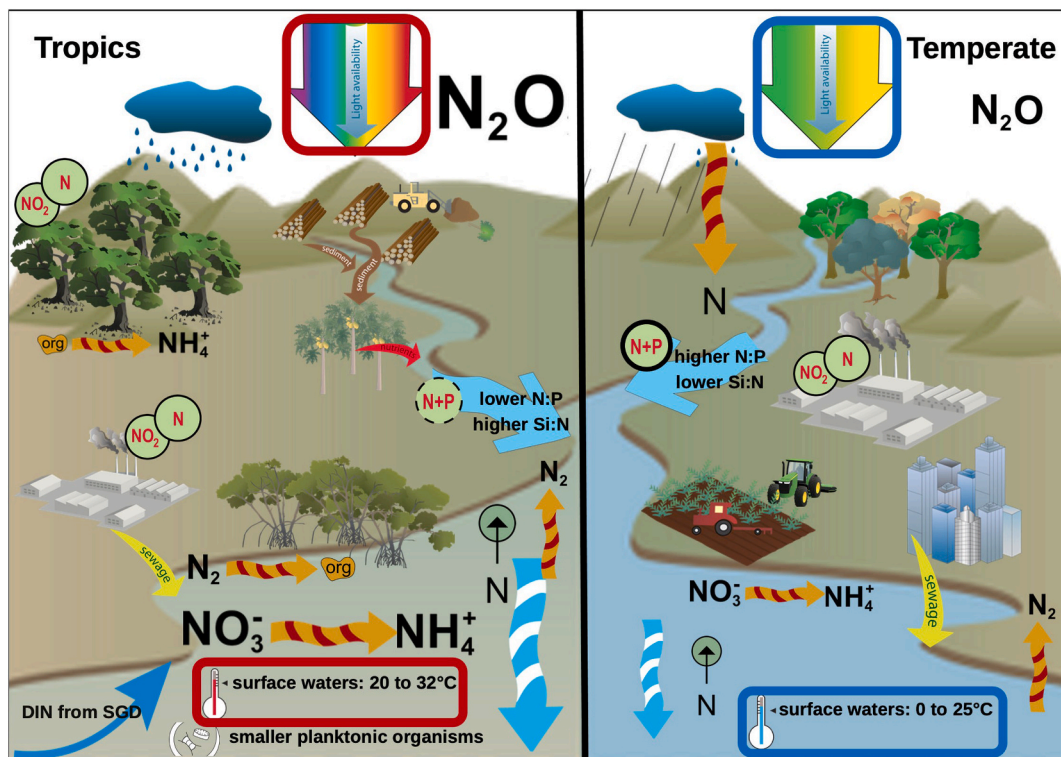


Fig. 1. Indicative graphical representation with some key differences in the environmental conditions and nutrient cycling in tropical and temperate coastal waters. Arrows indicate fluxes while the size indicate relative magnitude. The difference in solar radiation, surface water temperatures, river nutrient input ratios, export of riverine material to the open ocean (Blue/white arrows), ground water (SGD) dissolved inorganic nitrogen (DIN) inputs, atmospheric inputs (shown as precipitation), nitrogen fixation (Yellow/reds arrow from N_2 to org.), plankton organisms size, system retention of nitrogen (arrow inside green dot), nitrous oxide (N_2O) flux, dissimilatory nitrate reduction to ammonium (DNRA yellow/red arrow from nitrate (NO_3^-) to ammonium (NH_4^+)) are indicated. Boxes around solar radiation and surface water temperatures are used to indicate the key difference in these environmental variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

been shown to affect multiple food web components relevant for N and P cycling. These include decreased plankton cell sizes (Morán et al., 2010, 2020), accelerated phytoplankton blooming (Sommer and Lengfellner, 2008), and reduced total plankton biomass and changed community composition (Flombaum et al., 2013). In temperate waters, it has also been shown that increasing temperature changes the composition of organic matter produced by phytoplankton (Engel et al., 2011; Hueete-Stauffer et al., 2017), and stimulates the rates of microbial respiration and growth (Hueete-Stauffer et al., 2017; Morán et al., 2018). Therefore, in theory, when moving from temperate towards tropical regions similar changes should occur, but these may be obscured by factors such as changed species composition and subsequent food web interactions, and differences in nutrient limitation.

The temperature sensitivity of biological processes is typically expressed as an increase in the rate following a 10 °C change (Q_{10}) in temperature. The Q_{10} coefficient can vary widely, commonly for N- and P-related processes between 1.7 and 5, depending on both the environmental conditions and the biological processes investigated (e.g. Bissinger et al., 2008; Lønborg et al., 2018b; Rose and Caron, 2007). But generally, it is assumed that nutrient cycling should be faster in tropical than temperate systems, with a relatively larger difference for N than P (Lønborg and Álvarez-Salgado, 2012; Lønborg et al., 2009). However, different biogeochemical processes can exhibit different temperature sensitivities and optima: for example, in subtropical estuaries, it was recently shown that nitrite oxidation to nitrate has a lower temperature optimum than ammonium oxidation to nitrite, leading to summer-time nitrite accumulation (Schaefer and Hollibaugh, 2017). Resolving the responses of individual rates to predicted future warming is particularly important in the tropics, as these waters already have the highest surface water temperatures globally.

Elevated temperatures also promote stronger thermal stratification in tropical systems, which prevents vertical mixing and results in lower surface-water nutrient levels. This typical tropical water-column structure also increases the exposure to UV radiation and leads to primary production shifting to deeper in the water column (Burford et al., 2009). Elevated temperatures can also cause rapid evaporation in tropical coastal waters, allowing for “hypersaline” waters to form (Andutta et al., 2011; Wang et al., 2007), affecting processes such as gas solubility and air-sea fluxes.

In addition to temperature, sunlight has a lower seasonal amplitude in tropical coastal waters than temperate areas (the apparent “endless summer”; Kilham and Kilham, 1990). The sunlight intensity at the surface depends on multiple factors, including latitude, season and atmospheric conditions (e.g. cloud cover, dust, pollution and tropospheric ozone) (Pfeifer et al., 2006), the combined effects of which are that the highest irradiance is received near the margin of the tropics (Landsberg, 1961). Overall, the incident photosynthetically active radiation (PAR: 400–700 nm) is higher in the tropics and also more constant (Fig. 1), as the variation in day length is shorter (<30 min at the equator) compared to temperate systems (≈ 4 h) (Lewis, 1987). This should in theory lead to more constant seasonal primary production rates and the associated cycling of nutrients, but studies determining whether this indeed is the case are still lacking. Moreover, tropical latitudes receive higher ultraviolet (UV) radiation because of higher solar zenith angles and relatively lower ozone levels compared to temperate regions (Bernhard et al., 1997), which impacts e.g. organic nutrient cycling (see Section 4.1). The actual light intensity and spectral characteristics within the water column are also determined by the concentration of light-absorbing and -scattering substances in the water. The penetration depth of UV and PAR can vary greatly across both tropical and temperate waters

(Franklin and Foster, 1997). In oligotrophic tropical waters such as on coral reefs, UV penetration can be strongly controlled by coloured dissolved organic matter (CDOM) (Dunne and Brown, 1996; Zepp et al., 2008). Increased UV-light levels also can be harmful to planktonic organisms (Agustí et al., 2014), with photosynthetic organisms being more resistant than non-photosynthetic organisms (Llabrés et al., 2013). Some studies suggest that impacts of UV-light vary by latitude, with organisms in higher UV-light regions (tropics) generally being better adapted to higher UV levels (Agustí et al., 2014), suggesting potential differences in diversity and physiology of the organisms involved in nutrient cycling. Future projections also suggest that UV radiation levels will decline until the end of the 21st Century in temperate regions, but increase in the tropics due to decreasing ozone levels (Bais et al., 2011). This suggests a larger future role of photochemical processes in nutrient cycling in tropical coastal waters.

An aspect that will not be dealt with in detail in this review is how differences in the physical layout (geomorphology) influences the nutrient cycling in tropical and temperate coastal waters. In this regard, it should be noted that some types of coastal waters do not exist in tropical settings e.g. fjords, which are estuaries that have been/are being modified by land-based glacial ice (Perillo, 1995). Differences in the geomorphology clearly impact the processes mentioned in this review including nutrient groundwater inputs, burial, and denitrification. One important aspect of the geomorphology is the absence/presence of suitable sedimentation areas that influence the nutrient burial rate, sediment type (e.g. sand, mud) and organic carbon input which in turn impacts the overall benthic denitrification (Jickells et al., 2014). The layout of coastal waters can also influence properties such as stratification and mixing, and determine the extent to which shallow versus deep water primary production contributes to the overall system productivity. The geomorphology of coastal water can also influence properties such as the water column turbidity, which e.g. affect primary production by changing the light climate (Weston et al., 2008). However, as the geomorphology is highly variable at the system to system level, it is clear that a single model is not adequate to describe the unique and complex character of different coastal systems in tropical and temperate waters.

3. Nutrient inputs

Coastal waters continuously receive nutrients from a whole range of both external and internal sources, with the relative importance of each varying both locally and over larger scales. The following sections will outline the major nutrient input pathways and how these vary between tropical and temperate coastal waters.

3.1. Riverine inputs

Rivers provide the largest input of inorganic and organic nutrients into coastal waters. These nutrient fluxes are controlled by vegetation (especially N fixing species) and soil type, land use, precipitation, temperature, catchment slope, wetland cover, river floodplain extent, and biogeochemical processing in the river systems (Harrison et al., 2005; Mulholland, 2003; Seitzinger et al., 2010). Tropical rivers account for 55–64% of global total N and P export to coastal waters, but with large differences between tropical regions (Mayorga et al., 2010). Anthropogenic land use has increased riverine nutrient fluxes in most parts of the world. Conversely, dam construction has reduced particulate nutrient fluxes and may also promote a loss of fixed N from oxygen-depleted sediments (Maavara et al., 2017; Seitzinger et al., 2002a). Even though an important fraction of the anthropogenic nutrient input via rivers occurs in the tropics (Seitzinger et al., 2010), downstream impacts, such as plankton blooms, may be lessened or delayed due to a large dilution by riverine and ocean water resulting in little long term accumulation in the system (Eyre, 1997; Jennerjahn, 2012).

Catchment areas of tropical rivers have different vegetation

communities, soil types, geological history, flow regime and geomorphology, and more intense rainfall and runoff than temperate systems (Dai and Trenberth, 2002). To what extent this leads to differences compared to temperate regions in mean nutrient fluxes into the receiving coastal systems is still unresolved. Tropical forest soils are generally more weathered, and therefore, often experience P scarcity (Cleveland et al., 2011; Turner et al., 2018) and typically contain less organic matter because of higher microbial turnover. In contrast, they are relatively rich in N due to the higher abundance of N-fixing plant species, which may promote the production of phosphatase enzymes by plants and enable more efficient P retention (Pajares and Bohannan, 2016; Turner et al., 2018). Additionally, it has been suggested that tropical forest soils might experience higher acidity and variability in redox conditions, and that this potentially favours dissimilatory nitrate reduction to ammonium (DNRA) over denitrification, thus promoting N recycling over N loss (Pajares and Bohannan, 2016). Global watershed modelling originally indicated that tropical riverine N yields are very high due to (mostly natural) N fixation (Dumont et al., 2005). It is now thought that N fixation by tropical vegetation is balanced to a greater degree by denitrification, resulting in a downward revision of fluxes (Mayorga et al., 2010), although N yields especially in humid tropical regions are still relatively high, with natural N fixation often being the largest individual source (Mayorga et al., 2010; Seitzinger et al., 2010). While natural N fixation can also be the largest individual source in high-latitude regions (Compton et al., 2003; Hiltbrunner et al., 2014; Stewart et al., 2019), the N yield in high-latitude systems dominated by natural N fixation is typically lower than in tropical systems governed by natural N fixation (Dumont et al., 2005; Seitzinger et al., 2010).

Because of the higher weathering rates in the tropics, tropical rivers also generally have higher DSi concentrations, yields, and loads than temperate rivers, and contribute about 70% of the global Si export to coastal waters (Jennerjahn et al., 2006). Overall, terrestrial ecosystems in the tropics are inferred to deliver nutrients at relatively higher ratios of DSi:N to rivers and coastal waters, as compared to temperate systems (Fig. 1, Table 1; Downing et al., 1999; Eyre and Balls, 1999; Jennerjahn et al., 2006).

Comparing total N:P ratios in a limited number of tropical and temperate rivers, it was proposed that denitrification rates in tropical rivers were probably higher than in temperate rivers (Downing et al., 1999). Tropical freshwater systems are likely overall N-limited and deliver nutrients to coastal waters at N:P ratios close to or below the Redfield ratio of 16:1 (Table 1). Results from the global river nutrient flux model NEWS2 (Mayorga et al., 2010), suggest that tropical rivers on average (both discharge-weighted and non-discharge-weighted) have

Table 1

Mean \pm standard deviation for nutrient ratios in riverine nutrient loads estimated by the NEWS2 global river nutrient flux model for the world's exorheic basins (Mayorga et al., 2010). The ratios are shown for dissolved inorganic nitrogen (DIN), dissolved reactive silicon (DSi), total dissolved nitrogen (TDN), soluble reactive phosphorus (SRP), dissolved organic nitrogen (DON) and phosphorus (DOP), total dissolved phosphorus (TDP), particulate nitrogen (PN) and phosphorus (PP), as well as total nitrogen (TN) and phosphorus (TP). The results are shown both as discharge-weighted mean and standard deviation and without discharge-weighting (unweighted calculation).

Ratio	Discharge-weighted calculation		Unweighted calculation	
	Tropical Rivers	Non-Tropical Rivers	Tropical Rivers	Non-Tropical Rivers
DIN:DSi	0.4 \pm 0.7	0.8 \pm 1.3	0.4 \pm 1.1	0.6 \pm 1.4
TDN:DSi	0.6 \pm 0.9	1.3 \pm 2.2	0.5 \pm 1.4	1 \pm 2
DIN:SRP	54 \pm 94	77 \pm 121	209 \pm 779	368 \pm 881
DON:	40 \pm 4	42 \pm 6	42 \pm 13	44 \pm 15
DOP				
TDN:	42 \pm 21	50 \pm 23	51 \pm 35	61 \pm 35
TDP				
PN:PP	5 \pm 1	5 \pm 2	5 \pm 1	5 \pm 1
TN:TP	14 \pm 12	20 \pm 15	19 \pm 24	23 \pm 24

lower N:P ratios than non-tropical rivers, but higher DSI:N ratios (Fig. 1, Table 1), consistent with the hypothesis that denitrification in tropical soil and freshwater systems removes a substantial proportion of land-derived N. A recent latitudinal comparison of river systems in China found that (sub)tropical river sediments did have higher denitrification rates than temperate river sediments, but that DNRA rates were also higher at lower latitudes, suggesting faster rates of both N loss and recycling (Li et al., 2019). Estimated nutrient ratios also depend strongly on whether only dissolved or also particulate nutrients are included, with the average particulate N:P ratio far exceeding the Redfield ratio for both tropical and non-tropical rivers (Table 1). The bioavailability of particulate nutrients (and, indeed, of dissolved organic nutrients) is still poorly known and may vary with latitude (See also Section 4.1). Hence, it is unclear whether the riverine nutrient supply in the tropics is likely to promote different N and P limitation patterns compared to temperate systems, although the above ratios suggest that riverine nutrient delivery in the tropics helps to promote a state of N limitation of primary productivity in tropical coastal waters (but see also Section 4.2), in accordance with previous work (Burford et al., 2012; Jennerjahn, 2012).

Generally, rainfall is larger in the tropics due to the inter-tropical convergence zone (ITCZ), and rainfall generally has a more distinct seasonal pattern than in temperate systems (Pasricha and Fox, 1993; Syvitski et al., 2014). This often leads to a larger seasonal amplitude in delivering nutrients to tropical coastal waters (Araujo et al., 2014; Buck et al., 2019; McKee et al., 2000a, 2000b; Oehler et al., 2018). Seasonal flooding is also found to a larger degree in tropical systems characterised by distinct wet and dry seasons (Webster et al., 1998), and unpredictable floods may arise due to tropical storms, hurricanes, or cyclones (Covich et al., 2006). These events can transport large amounts of N, P, and sediment to coastal systems and cause massive resuspension events and short-lived (days to weeks) increases in primary production (e.g. Burford et al., 2012; Furnas et al., 2005).

First-flush effects, i.e. where the initial portion of run-off carries a disproportionately high concentration or flux of nutrients, are often associated with anthropogenic nutrient sources in urbanised catchments (Sansalone and Cristina, 2004). In tropical and subtropical regions with distinct wet and dry seasons, a seasonal first-flush at the onset of the wet season may be observed (Gao et al., 2018; Gunaratne et al., 2017; Yang et al., 2021). In tropical systems with a more even rainfall distribution, first-flush effects during individual rainfall events have also been reported (Chow and Yusop, 2014; Chua et al., 2009), but the more frequent rainfall in such regions can also weaken first-flush effects, which can complicate management measures to retain anthropogenic nutrients in tropical urban watersheds (Wang et al., 2017). Strong seasonality in nutrient fluxes is also observed at high latitudes (including in natural catchments) during spring snowmelt (Holmes et al., 2012; Jeannotte et al., 2020; Oczkowski et al., 2006). However, the effect of the spring snowmelt on nutrient fluxes can be modulated by basal ice in the soil, which limits the interaction between meltwater and soil and can reduce nutrient concentrations in rivers during the early melt period (Jeannotte et al., 2020; McClelland et al., 2014); this does not apply in tropical systems. The strength of first-flush effects (both seasonally and for individual storm events) across latitudes is very variable between different nutrients and catchments, and is not only controlled by hydrology but also by catchment characteristics (especially urban versus non-urban) and nutrient sources. For example, ammonia may show a stronger first-flush effect compared to nitrate in areas where ammonia is carried more in surface run-off but nitrate more in baseflow (Gao et al., 2018), although microbial ammonia oxidation in stream beds during dry periods can also drive a first-flush effect for nitrate (Merbt et al., 2016). In tropical systems where the shelf is narrow, most continental input is exported to the open ocean (Burns et al., 2008; Kineke et al., 2000; Kuehl et al., 2004), but where the shelf is broad, most riverine inputs are retained in wetlands, mangroves and the inner shelf, with only minor export to the open ocean (Brunskill, 2004; Mantoura et al., 1991). In general, as tropical systems are close to the equator, they experience a

reduced Coriolis force, which shortens the water residence time on the shelf. This leads on average to a more limited period for biogeochemical processing and a larger overall export of both river-derived and in-situ produced material to the open ocean compared to temperate systems (Fig. 1; Sharples et al., 2016).

Global change will impact river nutrient inputs, with studies suggesting that the largest increases in precipitation will be seen in the tropics (Fekete et al., 2010) and that the intensity, duration and frequency of tropical cyclones will increase (Knutson et al., 2010). Together with expanding human uses of coastal zones, this could increase the nutrient export from soils to tropical coastal waters, also given that tropical soils are typically fragile to disturbance (Finkl, 1999). Contrary to this, projected increases in dam construction, especially in river catchments of Asia, South America, and Africa (Lehner et al., 2011; Zarfl et al., 2015), will represent a sink for riverine organic matter due to settling and burial of particulate nutrients behind the dams, thereby likely reducing overall nutrient export (Maavara et al., 2017).

Overall, tropical coastal waters generally receive riverine nutrient inputs with lower N:P and elevated DSI:N ratios compared to temperate systems (Fig. 1; Table 2). The riverine delivery of nutrients in tropical systems has a bigger seasonal amplitude and a large part of river-derived material is exported to the open ocean compared to temperate system (Fig. 1; Table 2). Given that large uncertainty exists in riverine fluxes, future studies should focus on determining factors impacting nutrient fluxes and composition (inorganic versus organic) in tropical systems (Table 2).

3.2. Groundwater inputs

Coastal groundwater discharge, frequently described as 'Submarine Groundwater Discharge (SGD)', introduces substantial amounts of dissolved nutrients through permeable sediments or along karst conduits into coastal waters (Moore, 2010). On a global scale, tropical coasts export more than 56% (by volume) of terrestrial groundwater (Zhou et al., 2019). In the tropics, higher precipitation driven by the Walker Circulation (Jiang et al., 2021b) promotes the leaching of nutrients, especially dissolved inorganic N (DIN), from surface soils into deeper aquifers. A substantial proportion of phosphorus is retained on soil particles via adsorption, while the majority of DIN leaks into terrestrial groundwater (Santos et al., 2021b). On a global scale, DIN concentrations in coastal groundwater (both fresh and brackish) at 24 tropical study sites range from 2.6 to 1040 μM (median: 181 μM), with a major contribution of nitrate (Table S1). These values are comparable to the wide range found in subtropical zones (approximately 109–430 μM ; Leote et al., 2008; Null et al., 2012), and in temperate zones (63–260 μM ; Kim et al., 2013; Kroeger and Charette, 2008; Rocha et al., 2015).

Compared to offshore ocean water, groundwater in tropical regions has 2 to 3 orders of magnitude higher DIN concentrations (Fig. 2A), indicating a potentially large impact on the coastal DIN inventory from groundwater injection. Related to the soluble reactive P (SRP) and DSI concentrations, groundwater in tropical systems likely delivers excess N to coastal waters compared with the Redfield ratio (Fig. 2B and C). Coupled with hydraulic transport driven by a pressure gradient, wave-setup and tidal pumping (Santos et al., 2012), land-borne N rapidly injects into coastal systems via benthic systems (permeable sediments or karst conduits (Jiang et al., 2021a). Although a proportion of DIN is removed via denitrification or anammox in coastal aquifers (Erler et al., 2014; Jiang et al., 2018, 2021c), SGD-derived DIN still accounts for an important proportion of all external inputs (Ibanez et al., 2011). In particular, the magnitude of SGD-derived DIN fluxes ranges from 0.13 to 294 ton N d^{-1} (Table S1), which is comparable to tropical rivers at a local scale, such as the Rajang River, Malaysia (77.2 ton N d^{-1}), the Wanquan River, China (10.2 ton N d^{-1}), and the Pangani River, Tanzania (0.87 ton N d^{-1}) (Jiang et al., 2019). Accordingly, SGD can be an important source of DIN in several coastal systems, especially in semi-enclosed systems due to the long water residence time (Fig. 2D).

Table 2

Summary of the general differences and knowledge gaps in the nutrient cycling in tropical compared with temperate coastal waters. Please note that these possible impacts in some cases are theoretically based and will need further testing to quantify the specific difference.

	Pathway	Major Outcome	Major knowledge gaps
Nutrient inputs	Riverine	<ul style="list-style-type: none"> Lower N:P and elevated DSi:N ratios Larger seasonal amplitude More river-derived material reaches the open ocean 	<ul style="list-style-type: none"> Further estimates needed to decrease uncertainty in global fluxes Determine factors governing nutrient fluxes and composition in the tropics
	Coastal groundwater	<ul style="list-style-type: none"> Higher input 	<ul style="list-style-type: none"> Quantify spatial and temporal variations in inputs Determine impact of extreme weather on fluxes
	Lateral fluxes	<ul style="list-style-type: none"> Still unresolved 	<ul style="list-style-type: none"> Determine key processes controlling lateral fluxes Increase knowledge by synthesizing existing data
	Atmospheric deposition	<ul style="list-style-type: none"> Delivery is more efficient and rapid More important in oligotrophic waters 	<ul style="list-style-type: none"> Quantify if forms of N deposition vary between climatic zones Increase spatial-temporal measurements of deposition in tropics
	Nitrogen fixation	<ul style="list-style-type: none"> Still unresolved 	<ul style="list-style-type: none"> Establish if importance varies between the climatic zones Determine contribution of sedimentary nitrogen fixation
Recycling	Organic nutrients	<ul style="list-style-type: none"> Organic nutrient bioavailability is similar Larger importance in sustaining productivity Photochemical processes have larger importance 	<ul style="list-style-type: none"> Quantify spatial-temporal changes in organic nutrient bioavailability Measure impacts of photochemistry on organic nutrient bioavailability Increase estimates of particulate nutrient bioavailability
	Primary production and respiration	<ul style="list-style-type: none"> Benthic microalgal production is higher Peaks in productivity mainly linked with nutrient inputs 	<ul style="list-style-type: none"> Establish if production and respiration varies between climatic zones Determine whether metabolic state and nutrient limitation vary between climatic zones
	Sedimentary burial	<ul style="list-style-type: none"> Lower sediment burial Higher phosphorus burial efficiency 	<ul style="list-style-type: none"> Increase spatial resolution of burial estimates in both climatic zones
	Denitrification and Anammox	<ul style="list-style-type: none"> Denitrification, anammox, DNRA and N₂O fluxes are higher 	<ul style="list-style-type: none"> Determine thermal optimum for anammox Establish direct effects of temperature on processes

On a global scale, DIN delivery estimates from SGD range from 1.4 Tg N y⁻¹ (Beusen et al., 2013) to 32.2 Tg N y⁻¹ (Santos et al., 2021b). Among all the available estimates, tropical zones are frequently identified as those receiving the largest SGD inputs of DIN (Fig. 1), especially in Southeast Asia, India, and Mexico (Beusen et al., 2013). The DIN in groundwater is usually derived from several sources. In the tropical zone, some studies highlight the dominant contribution of chemical fertiliser leakage from farming systems (Rasiah et al., 2010), while others demonstrate that terrestrial organic matter degradation under the high temperature also makes an important contribution (Jiang et al., 2019). But in general the accumulation of nutrients, especially DIN, in terrestrial groundwater is linked to industrial and urban activities. For instance, sewage lost through leaking pipes into soils and interactions between sewage-polluted surface water and terrestrial groundwater in riparian zones add anthropogenic DIN to terrestrial groundwater (Lapointe et al., 2005). During the past twenty years, the population in tropical coasts, especially in South/South-East Asia, have shown a more rapid increase than in temperate zones (<https://data.worldbank.org/>). This growing human population increases agricultural pressures (such as oil palm plantations) and accelerates land-use changes (deforestation and urbanisation). Currently, the median value of DIN concentration in groundwater is comparable between the tropical and temperate zones (Table S1), while the peak value is higher in tropical coasts, revealing the human pressure. Coupled with the contribution from population increases, coastal groundwater DIN concentrations in tropical coasts might be continuously elevated in the future and thereby increase SGD-borne DIN inputs. Therefore, the role of SGD in delivering DIN should receive more attention from coastal managers and researchers.

In summary, though similar nutrient levels in terrestrial groundwater are found between these two zones based on the historical records, the magnitude of SGD-derived nutrient input in tropical zones is higher than the fluxes in temperate zones (Fig. 1; Table 2). Moreover, the difference in the SGD-borne nutrient input between tropical and temperate zones is projected to increase in the future due to population increase. Given the potential ecological and environmental impact in receiving systems caused by SGD-borne nutrients, future studies should improve the understanding of both spatial and temporal variations in SGD-derived nutrients along tropical coasts and pay particular attention to the magnitude of N and P input during extreme weather events (Table 2).

3.3. Lateral nutrient fluxes

Lateral nutrient fluxes occur in both tropical and temperate intertidal areas at three scales: 1) within a single vegetated ecosystem; 2) between vegetated and/or unvegetated ecosystems within the coastal landscape; and 3) between coastal and terrestrial and/or marine zones. Nutrient fluxes and budgets within a single ecosystem (Scale #1) have been defined for mangroves (Alongi, 2013), saltmarshes (Childers et al., 2000) and seagrasses (Romero et al., 2006), and studies exist for mudflats (Cook et al., 2004). The degree to which these ecosystems are connected (Scale #2) has been well researched in temperate locations (e. g. Wolaver et al., 1980), and is now an avenue of research that has gained importance in the tropics (Gillis et al., 2015). Between coastal and their adjacent terrestrial and/or marine zones (Scale #3), coastal wetlands often serve as an essential conduit transporting nutrients in both directions, serving as a buffer for land-derived excess nutrients, and/or as a source of nutrients to the marine zone.

Nutrient fluxes from vegetated coastal ecosystems are often discussed in terms of the outwelling hypothesis, where wetland primary production is greater than that used or stored in the system, with the excess exported to other coastal ecosystems or the wider coastal zone (e. g. Lee, 1995; Odum, 1968). While the spatial extent (Taillardat et al., 2019) and magnitude of outwelling has been debated (Alongi, 2013; Alongi et al., 2004; Santos et al., 2021a; Taylor and Allanson, 1995), it is more complex than the simple export of nutrients, and several processes

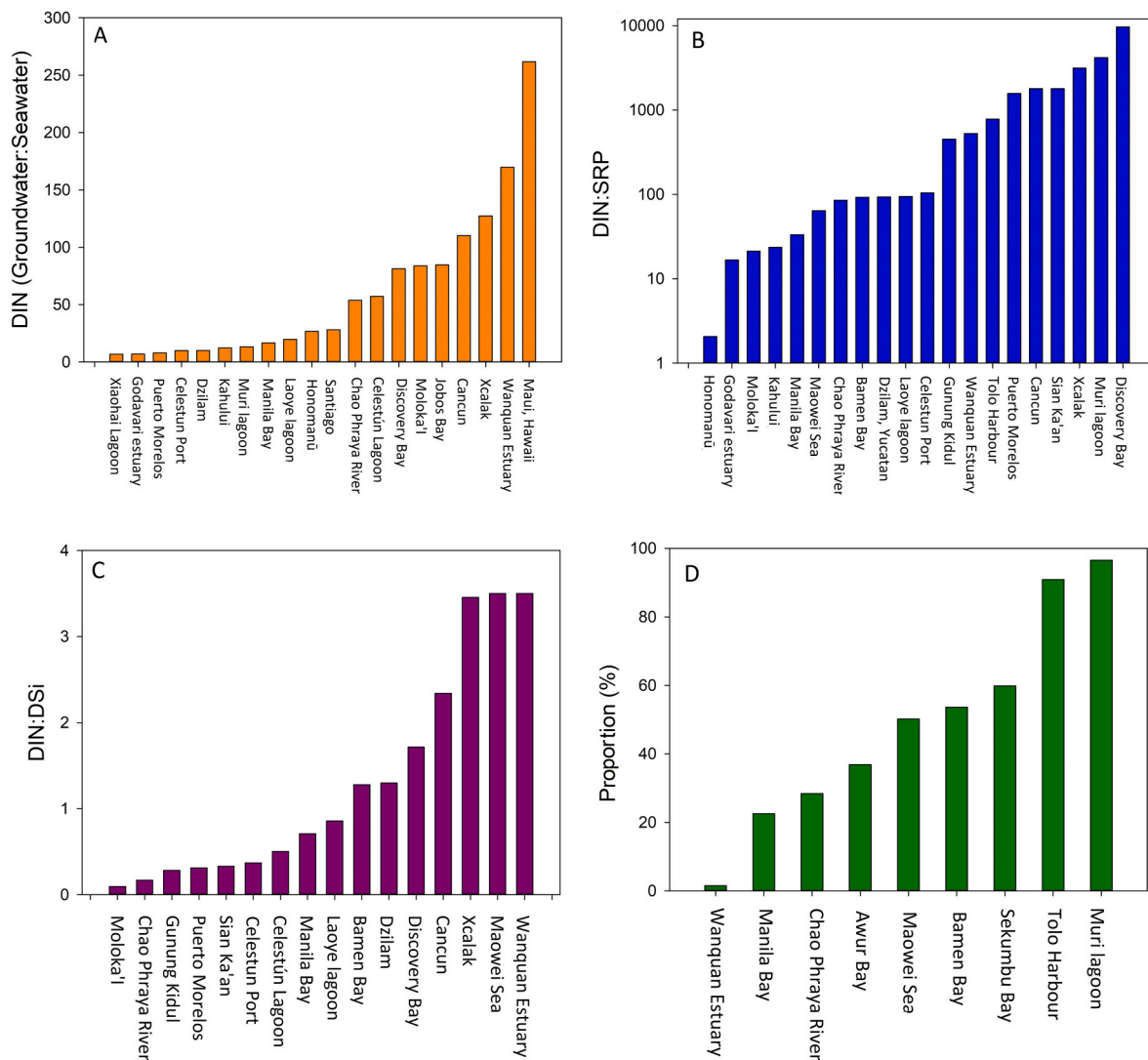


Fig. 2. (A) Comparison of dissolved inorganic nitrogen (DIN) concentration between coastal groundwater and offshore seawater in the tropical zone; (B) Concentration ratio between DIN to soluble reactive phosphorus (SRP) in coastal groundwater (fresh water) in the tropical zone; (C) Concentration ratio between DIN to dissolved reactive silicon (DSi) in coastal groundwater in the tropical zone; (D) Proportion of SGD borne DIN in total exogenous pathways in the study sites (e.g. river input and/or sewage). All sites are included in [Table S1](#).

can affect such lateral fluxes. These are likely to include, but are not limited to the type of adjacent/upstream systems, geomorphic system and tidal regime, nutrient type and chemical form, and precipitation ([Adame and Lovelock, 2011](#); [Adame et al., 2010](#); [Wilson and Morris, 2011](#)). For many of these processes, we still lack a comprehensive understanding of their influence, particular in tropical coastal wetlands. Knowledge of the outwelling hypothesis and the factors affecting it are better known in temperate wetlands, in part because temperate salt marshes were the origin of the hypothesis ([Odum, 1980](#)).

Several physical and ecological variables differ between the temperate and tropical zones, which will affect the direction, magnitude and importance of lateral fluxes: namely temperature, seasonality, dominant vegetation type, and the role of the benthic community. Temperature increases nutrient cycling rates (see [Section 1.2](#)) and strongly impacts the biogeochemical processes that moderate lateral fluxes. Seasonality heavily affects both pulses in supply but also drives nutrient demand ([Wolaver et al., 1980](#)). Temperate salt marshes mostly go dormant during cooler months, with lateral nutrient fluxes shifting in their direction and magnitude, but experience large pulses in demand in the growing season ([Wolaver et al., 1980](#)). In the (sub)tropics, monsoonal patterns may result in the flushing of nutrients both from

within systems and upland/upstream areas with increases in precipitation ([Alongi et al., 2004](#); [Rivera-Monroy et al., 1995](#)), but may also yield changes in demand. Finally, key differences in dominant vegetation type occur with latitude, with woody mangroves dominant in the tropics and herbaceous saltmarshes prevalent in temperate regions ([McKee et al., 2012](#); [West, 1977](#)), with a spatial overlap in these systems along many subtropical and some warm temperate coastlines. Dominant vegetation type can strongly influence the route by which primary productivity is stored, degraded, and exchanged between coastal ecosystems ([Martin and Moseman-Valtierra, 2015](#); [Simpson et al., 2019](#)). As one example, mangrove vegetation is heavily lignified, which is more resistant to enzymatic breakdown. This affects the ratio of various polymers produced during degradation ([Romero et al., 2005](#)), and means that mangrove detritus is substantially more lignified than salt marsh detritus ([Ouyang et al., 2017](#)). Thus, the ratio of nutrients transported between coastal ecosystems or utilised by coastal organisms will differ between the tropics and the temperate zone.

In conclusion, similarities between tropical and temperate lateral fluxes at all scales include their important role in mediating exchange, while key differences between tropical and temperate systems include impacts of temperature, seasonality, and vegetation type impacts on

exchanges, and their subsequent impacts on outwelling (Table 2). Future studies should focus on further characterising the key unifying processes that control lateral fluxes within and between regions as well as within the broader seascape and work to synthesize existing data (Table 2). A recent study (Alongi, 2020a) offers perhaps the most comprehensive review of comparisons between tropical mangroves and temperate salt marshes as well as differences in carbon lateral fluxes highlighting key differences. This work should be expanded upon for both carbon and other lateral nutrient fluxes. Tropical systems such as mangroves have received strong recent research attention through the lens of 'blue carbon', and there is scope to more strongly link blue carbon to theories of outwelling (*sensu Santos et al., 2021a*), and hence increase our knowledge for mangroves.

3.4. Atmospheric deposition

Anthropogenic emissions of oxidised and reduced N species have increased global atmospheric N deposition. Oxidised N species (nitric oxide/nitrogen dioxide) are mainly formed during combustion processes, with fossil fuels and biomass burning as major sources. Reduced N (principally ammonia) is emitted primarily by livestock farming. There is also organic N in the atmosphere, which deposits as dissolved organic nitrogen (DON) in precipitation, but the origin and processing of this organic N are currently not well understood (Jickells et al., 2017).

The highest atmospheric N concentrations are associated with larger cities, industry and agriculture, with the peak concentrations of inorganic N in tropical wet deposition being lower than in temperate regions (Jiang et al., 2021b). Historically, atmospheric N deposition has been greatest in North America and Europe, with temperate East Asia (especially China) gaining in importance over the past few decades (Ackerman et al., 2019; Kanakidou et al., 2016; Reay et al., 2008). However, large amounts of N deposition are also seen in tropical regions, especially in South and South-East Asia, and to a lesser extent in tropical Africa and South America. Biomass burning is probably an important source of N deposition in tropical regions (Ackerman et al., 2019; Kanakidou et al., 2016). Deposition of reduced N and organic N is also crucial in the tropics, reflecting agricultural and biomass burning sources (Doney et al., 2007; Kanakidou et al., 2016). It has been suggested that the atmospheric Walker circulation in the tropics might make the delivery of terrestrial atmospheric materials to the adjacent oceans more efficient and rapid, potentially increasing the fraction of atmospheric nutrients deposited at sea versus on land in the tropics (Jiang et al., 2021b).

While global models provide a relatively clear picture of the large-scale patterns of N deposition, the importance of atmospheric deposition for the nutrient budgets in coastal systems can be highly variable. Atmospheric N deposition can be an important source for coastal waters close to major atmospheric emission sources, such as North America and Europe (Howarth, 2007; Jickells, 2005), but negligible in regions where deposition is lower or other sources are more important. Even though East Asia has become one of the global hotspots for atmospheric N deposition, and now contributes substantially to N budgets in the North Pacific Ocean (Kim et al., 2014) and South China Sea (Ren et al., 2017), coastal N budgets are generally still dominated by riverine and other point sources. For example, atmospheric N only contributes around 10% of total N inputs in Jiaozhou Bay, China (Xing et al., 2017). It should be noted that estimating the magnitude of atmospheric N deposition to coastal waters is complex, and even where monitoring networks exist, they may not have sufficient resolution to yield accurate estimates due to large spatial differences and high variability in atmospheric circulation and dynamics (Loughner et al., 2016). Contrary to riverine inputs, which are point-sources, atmospheric deposition reaches surface waters directly and largely bypasses estuarine nutrient filters. Also, N deposited on land can partly leach into rivers and be carried to coastal waters. The importance of N deposition for a coastal system then depends on the area of water and the catchment characteristics and N retention on land

(Howarth, 2007). As many forests in temperate regions are N limited, a substantial proportion of deposited N may be lost to absorption by plants and denitrification in soils (Howarth, 2007). Since tropical forests are typically considered more N replete but P-poor (Pajares and Bohannan, 2016), it is tempting to speculate that export of N deposited on land might be more efficient in tropical systems, while lower background concentrations of nutrients in tropical coastal waters could make moderate sources of N relatively more important than in temperate coastal waters.

Given the lack of deposition measurements in tropical regions, there are few estimates of the importance of N deposition in specific systems. In the Caribbean, it was suggested that atmospheric N deposition (likely originating from continental North America) might account for up to 20% of the new N requirement by macroalgae in reefs in the Bahamas (Barile and Lapointe, 2005). More dramatically, atmospheric deposition contributed the majority of new N inputs to a coastal site off central Cuba, exceeding the estimated rates of N fixation (González-De Zayas et al., 2011).

It is possible that a greater contribution by biomass burning and agricultural emissions results in a greater proportion of reduced and organic N compared to oxidised N being deposited in tropical compared to temperate regions (Table 2). Moreover the delivery of atmospheric nutrients from land to the adjacent oceans may be more efficient and rapid in the tropics (Fig. 1; Table 2). Also, given the generally lower background concentrations of macronutrients in tropical waters, atmospheric deposition might be more important for tropical systems even at lower deposition rates than in temperate systems. Owing to the paucity of deposition measurements in the tropics, better spatial and temporal data on atmospheric N deposition are urgently needed (Table 2).

3.5. Nitrogen fixation

Temperature has been suggested as the primary control on global N₂ fixation, but irradiance is potentially also a limiting factor, since N₂ fixation is very energy-intensive (Breitbarth et al., 2007; Capone et al., 1997). Concentrations of iron, P and carbon dioxide (CO₂), and co-limitation between them, can also impact N₂ fixation rates (Boyd et al., 2010). Traditionally, it has been assumed that marine N₂ fixation was primarily important in the tropics, based on the expectation that higher sunlight levels, warm temperatures, lower turbulence, and lower availability of inorganic N would favour N₂ fixation. However, this paradigm is currently being revised: it is becoming clear that the diversity and geographic range of N₂ fixing pelagic microbes is much larger than previously believed, and benthic N₂ fixation is increasingly recognised to be important in both temperate and tropical environments (Zehr and Capone, 2020). Numerous studies have shown that pelagic N₂ fixation also occurs in temperate (Bentzon-Tilia et al., 2014; Mulholland et al., 2019; Rees et al., 2009) and even polar (Shiozaki et al., 2018, 2020) regions, and that temperate coastal waters may be particularly important sites of N₂ fixation (Messer et al., 2021; Tang et al., 2019). In tropical waters, the cyanobacterial genus *Trichodesmium* and *Richelia* endosymbionts of diatoms are key pelagic N₂ fixers. Blooms of *Trichodesmium* are found in tropical coastal waters around the world (Blondeau-Patissier et al., 2018; Carvalho et al., 2008; Dias et al., 2020; Lugomela et al., 2002), and seasonal peaks seems to be linked to reduced turbulent mixing, which tends to break up the bundles formed in the bloom (Revelante and Gilmartin, 1982). In addition to providing nutrients, tropical river plumes may also stimulate N₂ fixation by supplying limiting micronutrients (e.g. iron), as reported for the Amazon River plume (Subramaniam et al., 2008), the Congo River plume (Foster et al., 2009), and the Mekong River plume (Grosse et al., 2010).

In coastal waters, most N₂ fixation appears to be benthic (Capone, 1988; Voss et al., 2013), and is likely critical for sustaining the productivity of coral reefs, seagrasses (both temperate and tropical) and mangroves (Voss et al., 2011 and references therein). In subtropical Moreton Bay, Australia, N₂ fixation accounts for 70% of the N input and

most of this is benthic N_2 fixation (Eyre and McKee, 2002; Wulff et al., 2011). Seagrass meadows are important sites for N_2 fixation in both temperate and tropical waters, but N_2 fixation rates in tropical seagrass beds appear to be higher (Herbert, 1999). Sulphate-reducing bacteria in the rhizosphere may be particularly important for N_2 fixation in seagrass meadows (Welsh, 2000), but epiphytic microbes contribute as well (Cardini et al., 2018).

N_2 fixation associated with scleractinian corals has received a lot of research interest recently and clearly contributes to coral holobiont nutrition (Benavides et al., 2017; Glaze et al., 2021), although at the reef scale, N_2 fixation by microbial mats, turf algae, and sedimentary microbes probably contributes more new N than corals (Cardini et al., 2016; O'Neil and Capone, 1989). Given this diversity of different habitats within a reef, N_2 fixation rates can vary a lot over small scales between different reef substrates, and whole-reef estimates of N_2 fixation are therefore rare (Cardini et al., 2016; Larkum et al., 1988). While N_2 fixation is thus clearly a significant part of reef N budgets and likely critical for the functioning of coral reefs (Benavides et al., 2017), better estimates of whole-reef N fixation rates are clearly needed.

High variability in rates between different substrate types also complicates the assessment of N_2 fixation for mangrove ecosystems, where N_2 fixation takes place in the sediments, associated with microbial mats, but also on the bark and above-ground roots of mangrove trees (Alongi, 2020b; Voss et al., 2011). Current estimates of whole-system N_2 fixation rates in mangroves cannot account especially for N_2 fixation associated with mangrove trees themselves, and are therefore likely underestimates (Alongi, 2020b).

Recently, it was reported that N_2 fixation by heterotrophic sulphate-reducing bacteria supplied as much or more N than urban run-off and sewage in a strongly eutrophic urban tropical estuary (Oczkowski et al., 2020). Here, anthropogenic increases in organic matter input appeared to stimulate heterotrophic N_2 fixation, thereby amplifying the N pollution. While this finding reinforces the need for further studies in tropical coastal waters to better understand nutrient cycle feedback processes, it is also being recognised that sedimentary N_2 fixation may be considerably more important in temperate coastal waters than previously recognised. This reappraisal of the importance of sedimentary N_2 fixation by heterotrophs in temperate environments raises the possibility that tropical and temperate systems might not be as distinct in terms of N_2 fixation as previously believed.

In summary, although N_2 fixation is clearly important in tropical coastal systems, we still lack good estimates of whole-ecosystem N_2 fixation rates especially in ecosystems such as coral reefs and mangroves where N_2 fixation by different microbial communities takes place in different parts of the system. The increasing recognition of significant N_2 fixation rates in temperate coastal waters additionally suggests that there might be less of a systematic difference in N_2 fixation rates between temperate and tropical zones than previously thought (Fig. 1; Table 2). Future studies need to focus on obtaining better whole-system N_2 fixation rate estimates for complex tropical ecosystems such as coral reefs and mangroves, as well as aim to better constrain the poorly understood, but likely very important, contribution of sedimentary N_2 fixation in both tropical and temperate coastal waters (Table 2).

4. Recycling

Nutrients in coastal waters are affected by inputs and recycling in both the water column and sediments. These recycling processes dependent both on environmental conditions (e.g. temperature, sunlight) as well as the quantity and composition of the inputs. In the next sections we will outline major differences in recycling pathways between tropical and temperate coastal waters.

4.1. Cycling of organic nutrients

Primary production using recycled nutrients is fundamentally

dependent on the degradation of organic nutrients. Organic nutrients, here defined as the sum of particulate and dissolved organic nutrients, in coastal waters originate from both internal (e.g. plankton) and external sources (e.g. rivers) (Lønborg et al., 2020; Raymond and Spencer, 2015).

The main biological sink for dissolved organic nutrients are heterotrophic bacteria (Lønborg and Søndergaard, 2009). Contrary to inorganic nutrients, not all particulate and dissolved organic nutrients are available for microbial utilisation over time scales (days) relevant for their growth. However, the bioavailable part can be degraded over time scales of days to months (e.g. Lønborg and Álvarez-Salgado, 2012). Larger organisms are generally not able to directly take up dissolved nutrients, but both living and detrital ("non-living") particulate nutrients can act as a food source for zooplankton, fish, suspension-feeders (e.g. bivalves) and other benthic organisms (e.g. gastropods) (Wilson and Bellwood, 1997; Wilson et al., 2001). Due to all the processes involved in the cycling of organic nutrients, generalisations about difference and similarities in temperate and tropical zones are challenging.

Terrestrially derived organic nutrients traditionally have been assumed to be essentially non-degradable by marine microbes, but this view has changed over the last decades (Sinsabaugh and Findlay, 2003), with studies showing that organic matter can be degraded within days to weeks in tropical systems such as the Amazon River (Ward et al., 2013, 2017). The transport of terrestrial organic nutrients from freshwater to seawater can increase organic matter bioavailability due to changes in the ionic strength of the water (Wikner et al., 1999). Other studies have also shown that the bioavailability of organic nutrients depends on the nature of terrestrial sources (land use), with anthropogenic sources being more bioavailable than organic nutrients exported from natural catchments (Seitzinger et al., 2002b). A fraction of the organic matter received is in the form of CDOM and absorbs sunlight (Lønborg et al., 2021). This absorption initiates a range of photochemical processes with studies demonstrating that the exposure of terrestrial organic nutrients to sunlight (See Section 2) can increase (Moran et al., 2000; Moran and Zepp, 1997) but also decrease the bioavailability by competing with bacteria for substrate (Lønborg et al., 2016; Scully et al., 2003). The importance of these photochemical reactions in determining the bioavailability of terrestrial organic nutrients depends on the transparency of the receiving coastal waters, and previous exposure to sunlight (Vähätalo and Wetzel, 2004). Although most experiments have been conducted in temperate regions with a large riverine input, tropical rivers deliver about two thirds of the global riverine dissolved organic carbon (DOC) to the ocean (Raymond and Spencer, 2015). Due to the higher UV-light levels and high DOC inputs the potential impacts of these photochemical processes on N and P cycling might be higher in tropical systems compared to temperate areas, but this will also depend on the C:N:P stoichiometry of the organic matter. This topic clearly requires further investigation.

As many tropical coastal waters are oligotrophic, organic nutrients may play a larger role than inorganic nutrients in fuelling productivity (Lønborg et al., 2018a). Globally, $35 \pm 13\%$ and $59 \pm 29\%$ (average \pm SD) of the DON and dissolved organic P (DOP) in coastal waters is bioavailable to microbes (Lønborg and Álvarez-Salgado, 2012). At the same time, few bioavailability estimates exist for particulate N (PN) and phosphorus (PP), which have been obtained from mainly planktonic material and these are generally high ($75 \pm 6\%$ for PN, $90 \pm 3\%$ for PP; (Burkhardt et al., 2014; Lønborg et al., 2018a). Direct estimates of the bioavailability of organic nutrients are scarce in the tropics. A comparison with temperate waters can only be made for the dissolved fraction, as no comparable estimates are available for the particulate fraction. The few estimates in tropical coastal waters suggest that the dissolved organic nutrient bioavailability is similar to temperate zones (Lønborg, in prep), with P-containing compounds being more bioavailable than N compounds. A study in the tropical coastal waters of the Great Barrier Reef also suggests that organic nutrients (particulate and dissolved) contain around 90% of the total bioavailable N and P in this oligotrophic system (Lønborg et al., 2018a), testifying to their

importance in nutrient cycling in tropical coastal waters.

Cycling of organic nutrients in coastal systems is also a sedimentary process. For example, benthic degradation of organic N has been shown to provide 20–80% of phytoplankton N requirements (Herbert, 1999 and references therein). However, some shallow water bodies still have substantial pelagic (in-water-column) degradation (Damashek and Francis, 2017), and it is the dominant process in deeper oceanic waters. In nearshore coastal waters, sediments are particularly important because organic nutrients can be subject to recurrent resuspension into the water column by wind-wave action, bottom stress and turbulence from tidal currents, and bioturbation by organisms (Bianchi et al., 2018; Walker and O'Donnell, 1981). The organic nutrients can enter a cycle of resuspension, horizontal transport and sedimentation events, leading to reoccurring cycles of UV-light and bacterial degradation in the water column and sediments. But whether these impacts vary between tropical and temperate coastal waters is still unresolved.

Overall, organic nutrient bioavailability is similar in tropical and temperate regions (Table 2). However the relative importance of organic nutrients in sustaining productivity is larger in oligotrophic tropical coastal waters (Table 2). We hypothesise that due to the higher UV-light levels and organic inputs, the impacts of photochemical processes is likely higher in tropical systems compared to their temperate counterparts, but this requires further investigation (Table 2).

4.2. Primary production and respiration

Plankton primary production rates have been measured for centuries in temperate coastal waters. In comparison, relatively few measurements are available for tropical coastal waters, making it difficult to conclude whether rates vary systematically between tropical and temperate zones (Burford et al., 2008; Cloern et al., 2014). In contrast, even though only a few benthic microalgae production estimates are available for tropical waters, these are generally 3 to 4 times higher than in temperate regions (Cahoon, 1999; Kwon et al., 2020). The fate of benthic microalgal carbon and nitrogen has been well studied in e.g. temperate (Middelburg et al., 2000) and subtropical (Oakes et al., 2010) coastal sediments but never in tropical sediments. It is expected that benthic microalgal carbon in tropical sediment would have a similar fate as in other climate zones, which shows little difference from Arctic to subtropical (Oakes et al., 2016). In contrast, more benthic microalgal N would be expected to be recycled and lost to the atmosphere as N₂ in tropical coastal sediments due to higher temperatures. This in turn would increase sediment C:N ratios in tropical sediments compared to temperate sediments.

In tropical coastal waters, phytoplankton production rates are generally high as the factors fuelling productivity (e.g. nutrient supply, solar radiation) are relatively stable (Nittrouer et al., 1995), with production rates (e.g. mean of 1850 mg C m⁻² d⁻¹ in the Banda and Arafura Seas; Furnas and Carpenter, 2016; Gieskes et al., 1990) in some cases matching productive upwelling regions (i.e. upwelling season mean 1500 mg C m⁻² d⁻¹ in the Ria de Vigo; Álvarez-Salgado et al., 2009). In tropical lakes, high productivity despite low nutrient levels results from a tight coupling of production and degradation combined with higher light levels and temperatures (Lewis, 1996), but whether the same also applies for tropical coastal waters is currently untested.

In both tropical and temperate waters, differences in N, P, Si and micronutrient concentrations can influence the phytoplankton community composition with the dominance of autotrophic picoplankton, particularly picocyanobacteria, under nutrient-depleted conditions (Agawin et al., 2000). As macronutrient concentrations increase, larger phytoplankton, particularly diatoms, contribute more to the overall primary productivity (e.g. Furnas et al., 2005). To our knowledge, no study has systematically investigated whether the nutrient limitation of primary production varies between temperate and tropical coastal waters, but generally both seem to be N- rather than P-limited over small spatial and temporal scales (Howarth, 1980; Howarth et al., 1988),

while over larger scales, P can be limiting due to N₂ fixation (Eyre and McKee, 2002; Wulff et al., 2011).

As light is normally not limiting in tropical waters, except in turbid locations, seasonal spikes in productivity are more commonly driven by seasonal changes in nutrient input due to wind-driven circulation patterns or precipitation (López-Sandoval et al., 2021; Tomczak and Godfrey, 1994). In contrast, seasonal changes in primary production in temperate systems are chiefly linked to light availability (Smith et al., 1991).

Planktonic respiration in coastal waters is largely controlled by temperature, and the supply and quality of organic matter (Hopkinson and Smith, 2005; Pomeroy and Wiebe, 2001). Especially in systems with small external organic matter inputs, chlorophyll *a* — indicator for primary production—tends to be a better predictor of respiration rates than temperature (Hopkinson and Smith, 2005). The higher temperatures of tropical coastal waters also mean that oxygen has a lower saturation level; combined with higher respiration rates, this could potentially make tropical waters more susceptible to low or depleted oxygen ("hypoxia") levels than temperate systems. However, little is known about the likelihood and potential threat of hypoxia in tropical coastal waters, but one study has suggested that low oxygen might locally impact coral reef mortality (Altieri et al., 2017). But the overall importance of hypoxic conditions, and whether tropical coastal waters in reality are more susceptible to hypoxia than temperate systems, still needs to be investigated in detail.

The ratio of primary production to respiration indicates whether more organic matter is produced in a system than consumed (net autotrophic or net heterotrophic) (Smith and Hollibaugh, 1993). This ratio has been shown to vary depending on numerous factors including the input and composition of nutrients (Martínez-García et al., 2010), food-web structure (e.g. phytoplankton and zooplankton community structure and sizes; Ikeda et al., 2007; Maranon, 2015), and the amount and reactivity of the organic matter (e.g. Hopkinson and Smith, 2005; Lønborg and Álvarez-Salgado, 2012). Generally, systems with large inorganic nutrient inputs are autotrophic while those with lower inorganic and/or large organic inputs are heterotrophic (Hopkinson and Smith, 2005). Shallow coastal ecosystems, which are dominated by salt marshes, seagrasses, and mangroves tend to be autotrophic (Duarte and Cebrián, 1996; Hemminga and Duarte, 2008). In temperate coastal waters, both autotrophic and heterotrophic systems have been identified, while the few published measurements of pelagic metabolism from tropical coastal waters suggest that these can be balanced, autotrophic or net heterotrophic, with fast transitions between these metabolic states (López-Sandoval et al., 2019; McKinnon et al., 2007, 2013, 2017).

Generally, it is assumed that when substrate is not limiting, respiration tends to increase faster than primary production with rising temperatures (Yvon-Durocher et al., 2012). Consequently, it would be expected that tropical coastal waters should be more heterotrophic than temperate ones, but this is clearly often not the case (McKinnon et al., 2007, 2013, 2017). This could be due to the fact that respiration is substrate limited, as recently suggested for the Great Barrier Reef (Carreira et al., 2021; Morán et al., 2020), but it may also be an artefact of the limited number of measurements of temperature sensitivity in tropical waters.

In conclusion, benthic microalgal production is generally thought to be higher in tropical coastal waters compared to temperate waters (Table 2). Seasonal peaks in productivity in tropical coastal waters are mainly linked to nutrient input, while light availability is the main controlling factor in temperate waters (Table 2). Future studies should focus on determining whether production and respiration rates vary systematically between the tropics and temperate coastal waters (Table 2). Furthermore, it is essential to determine if the metabolic state and nutrient limitation of primary producers vary systematically between tropical and temperate coastal waters (Table 2).

4.3. Sedimentary nutrient burial

Sedimentary burial is a major pathway for nutrient loss in marine ecosystems. It is mainly controlled by oxygen exposure time, sedimentation rates and sediment/organic matter composition. Except for terrigenous sediments from river inputs, nutrient delivery to sediments is chiefly in the form of organic matter produced in coastal waters. Biogeochemical processes in the sediment transform organic N and P, resulting in either permanent burial or return to the water column by diffusion, advection, or sediment resuspension. Generally, tropical shelves appear to act as more efficient organic matter “furnaces” in comparison to temperate shelves, remineralising nearly all terrestrial and in-situ produced organic matter, with only minor sediment burial (Aller and Blair, 2006; Aller et al., 1996; Brunskill et al., 2002). This contradicts the paradigm that coastal systems are the primary storage reservoirs for organic matter and most terrestrial weathering products (Berner, 1982).

In oxygenated sediment layers (usually the top centimetres), organic matter is degraded aerobically, and organic N and P are converted to ammonium and phosphate, respectively. When oxygen is present, phosphate is readily adsorbed by iron (oxy)hydroxides, while N can diffuse back into the overlying water, either as ammonium or, following nitrification, as nitrate. However, in suboxic and anoxic sediment layers, nitrate can be denitrified and permanently lost from the system (See Section 4.4), while iron-bound phosphate re-dissolves into the pore water. Depending on the sediment depth and chemical composition, phosphate in the pore water can either be returned to the water column, or be re-precipitated as authigenic calcium fluorapatite (CFA), leading to permanent sedimentary burial. A key factor governing sedimentary dynamics of both N and P is whether or not the sediment is sulphidic (i.e. producing sulphides from sulphate reduction). The presence of sulphide inhibits denitrification, but permits the process of DNRA (Bernard et al., 2015; Domangue and Mortazavi, 2018), promoting N recycling over loss. Sulphate reduction also allows for iron-bound P to dissolve and re-precipitate as CFA (e.g. as found in the Black Sea; Dijkstra et al., 2018; Kraal et al., 2017), or as reduced iron minerals such as vivianite (Egger et al., 2015).

Tropical shelf sediments are often rich in calcium carbonate (CaCO_3), compared to the more terrigenous mineral deposits that dominate temperate waters. More than half of the total ocean CaCO_3 deposition takes place in shelf seas, and of that the majority is found in tropical and subtropical shelves (O'Mara and Dunne, 2019). CaCO_3 sediments are particularly efficient at sequestering P, both through the production of CFA and because phosphate adsorbs strongly to CaCO_3 particles (De Jonge and Villerius, 1989; Kraal et al., 2017; Monbet et al., 2007). For example, in the Great Barrier Reef, P burial efficiency was lower (around 60–70%) close to shore where sediments were dominated by terrestrial aluminosilicates, but increased to approximately 100% at offshore carbonate-dominated sites (Monbet et al., 2007).

Seagrasses and macroalgae growing in such carbonate-rich tropical sediments have, therefore, been suggested to be P-limited, for instance based on higher tissue N:P ratios (Lapointe et al., 1992; Short, 1987). However, it has been shown in seagrass beds that sulphide oxidation in the sediment can generate sufficiently acidic conditions to dissolve sedimentary CaCO_3 and thereby release carbonate-bound P, which becomes available for seagrass uptake (Jensen et al., 2009). The potential for release of P from carbonate sediments was also confirmed in coral reef sediments using chamber incubations (Sorokin, 1992; Suzumura et al., 2002), but the net exchange between sediments and the water column was extremely low in these experiments, suggesting that P released through this route can be efficiently taken up by benthic communities (Suzumura et al., 2002). At the same time, denitrification from carbonate sediments is significant (Eyre et al., 2013) and can also occur under sulphidic conditions in seagrass carbonate sediments (Van Dam et al., 2021), so it is not necessarily the case that N loss is inhibited under these conditions. Moreover, the capacity of carbonate sediments

to adsorb P also depends strongly on sediment grain size, with coarse carbonate sediments less likely to promote P limitation (Erfteimeijer and Middelburg, 1993). Although the majority of shelf-sea CaCO_3 deposition takes place in the tropics and subtropics (O'Mara and Dunne, 2019), terrigenous minerals are also widely found in tropical shelves affected by river input (Laugié et al., 2019).

Overall we hypothesise that tropical coastal waters are more efficient than temperate systems in organic matter degradation, which limits sedimentary nutrient burial (Table 2). Tropical waters with CaCO_3 -rich sediments may have a higher P burial efficiency compared with temperate coastal waters, although physical sediment characteristics and processes promoting carbonate dissolution strongly moderate the extent of P adsorption and the recycling and availability of P to benthic producers. Further measurements are needed to increase the spatial resolution of nutrient burial data both in tropical and temperate coastal waters (Table 2).

4.4. Denitrification and anammox

Denitrification and anammox transform bioavailable N to N_2 gas, which is lost to the atmosphere, thereby counteracting the N enrichment of coastal systems (Eyre and Ferguson, 2009). Denitrification also produces nitrous oxide (N_2O ; Murray et al., 2015), a potent greenhouse gas contributing to global warming and ozone-depletion (Ravishankara et al., 2009). However, in low-nutrient systems, as found in some tropical coastal waters, N assimilation is more important than denitrification, resulting in a net retention of N within the system (Fig. 1; Cook et al., 2004; Risgaard-Petersen et al., 2003).

Experimental studies across Arctic (Rysgaard et al., 2004), temperate (Zhou et al., 2014) and subtropical (Tan et al., 2020) systems have shown that denitrification rates in aquatic sediments increase with increasing temperature, with no thermal optimum up to the maximum of the experiments (around 35 °C). Although there are no experimental warming studies in tropical systems, studies from other climate zones suggest that denitrification rates should be higher in tropical regions due to higher temperatures, under similar environmental conditions (e.g. nitrate concentrations). Denitrification-driven sediment-water N_2O fluxes also increase with increasing temperature (Tan et al., 2020). This suggests that sediment-water N_2O fluxes should also be higher in tropical coastal waters, but this has not translated to higher N_2O concentrations in tropical estuarine water columns (Murray et al., 2015). Lower nitrate concentrations in tropical estuaries result in lower N_2O concentrations and lower (or negative) water-air N_2O fluxes (Murray et al., 2015, 2020).

Anammox rates also increase with increasing temperatures in Arctic, temperate and subtropical aquatic systems, but in contrast to denitrification, anammox rates have a thermal optimum (Rysgaard et al., 2004; Tan et al., 2020; Zhou et al., 2014). The anammox thermal optimum increases from 14 °C in Arctic sediments, to 25 °C in temperate sediments and up to 30 °C in subtropical sediments, which suggests that it may be even higher in tropical sediments.

Some studies have reported that DNRA is more important than denitrification when organic matter, salinity, and temperatures are elevated (Burgin and Hamilton, 2007; Giblin et al., 2013; van den Berg et al., 2015). High DNRA rates are potentially favoured in tropical climates because high temperatures can enhance organic carbon degradation by DNRA microbes (Giblin et al., 2010; Smyth et al., 2012). This leads to a dominance of DNRA over denitrification and anammox in many tropical regions, but this may also be due to indirect effects of temperature on nitrate concentrations (Fig. 1; Damashek and Francis, 2017; Dong et al., 2011). This has also been shown in tropical/subtropical, eutrophic estuaries in the Pearl River and Yangtze River in China (Bu et al., 2017; Yin et al., 2017), and in estuaries in Thailand and Indonesia (Dong et al., 2011), suggesting that N loss via denitrification and anammox versus recycling via DNRA might respond differently to warming in tropical coastal waters compared to their temperate

counterparts. One study also shows that the potential rates of denitrification and DNRA increased from temperate to tropical zones, but no change in anammox rates was detected (Li et al., 2019).

In summary, we hypothesise that denitrification, anammox, DNRA and sediment-water N_2O fluxes are higher in tropical than temperate coastal waters under similar environmental conditions (e.g. nitrate concentrations) due to higher temperatures (Fig. 1; Table 2). The thermal optimum for anammox is also expected to be higher, but this has not been measured in tropical coastal waters. Clearly, establishing the effects of temperature on denitrification, DNRA, and anammox and sediment-water N_2O flux rates in tropical sediments is an important area for further research (Table 2).

5. Concluding remarks and some future perspectives

Tropical and temperate coastal waters are critical for human societies but they are under increasing anthropogenic pressures. Determining similarities and differences in nutrient cycling is therefore relevant both from a research and a management point of view.

The comparisons of tropical and temperate coastal waters is not straightforward due to the very high natural variability within both latitudinal ranges, and the resulting wide range of physical, chemical and biological conditions. But in this manuscript we have outlined how similarities in the nutrient cycling of coastal waters across regions are present in some respects, but differences are also clearly evident (Fig. 1; Table 2). Most of the generalizations that can be made are, one way or the other, related to temperature and sunlight as well as precipitation levels and patterns. These differences are particularly important where they directly influence major fluxes and pathways with key processes including river nutrient inputs, organic nutrient degradation and primary production. The information presented in this manuscript begins to provide a clearer description of the biogeochemical processes in tropical coastal waters (Fig. 1; Table 2), but a more mechanistic view is currently needed. The research community therefore needs to recognize that tropical coastal waters are different compared to temperate ones, and that ecosystem understanding based on temperate regions cannot simply be transferred to tropical settings.

From this review it is also evident that larger gaps, uncertainties and limitations exist in our understanding of the biogeochemical processes in tropical coastal waters compared with temperate zones. For instance, we still need to answer basic questions such as why does temperature in some cases impact the productivity in tropical waters, while in others it does not (See Section 4.2). Generally, studies and observations of many basic biogeochemical parameters and their temporal/spatial importance and regulation are missing in tropical coastal waters. Cross-ecosystem and latitude experimental studies should be a critical next step towards understanding the importance of different environmental conditions (e.g. temperature) in controlling biogeochemical rates in both tropical and coastal waters more generally. To obtain a more mechanistic understanding of tropical coastal waters a fruitful research avenue could be to conduct focused process-orientated studies in representative locations, which could then be used to scale up process rates to larger areas.

Relatively few long-term observational datasets are available for tropical systems compared with temperate coastal waters, which hampers our understanding of the linkages between key factors such as climate forcing and river inputs. Furthermore, the data that do exist often do not include process variables such as primary productivity. These datasets are also often geographically restricted to easily accessible shallow shelf regions, which makes outer shelves and deeper waters poorly sampled and less understood. Furthermore, many of the relevant biogeochemical datasets collected in tropical waters are only available in “grey literature”, making it difficult to examine trends and gather data for synthesis work. Future international efforts therefore should ensure the availability of these valuable datasets not only for research purposes but also for obtaining a better and more well-informed management of

tropical coastal waters.

We hope that highlighting differences and similarities between tropical and temperate coastal biogeochemical cycles will stimulate new research ideas and hypotheses, challenge the research community and inspire further studies on biogeochemical cycles in tropical coastal waters. Obtaining further knowledge of these systems is essential for our ability to accurately understand and forecast impacts at local, regional, and global scales.

Author statement

CL and PM outlined the manuscript, and CL collated the original draft. All authors contributed to writing, reviewing, editing and approved the manuscript for publication.

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.

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Appendix A. Supplementary data

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