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The ecological consequences of nutrient enrichment in mangroves

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ABSTRACT

Mangrove forests are among the most productive ecosystems on earth, despite featuring trees that can grow in nutrient poor, highly saline environments with anoxic soils. Anthropogenic inputs of both nitrogen (N) and phosphorus (P) have increased due to agricultural, aquacultural, and urban runoff into coastal mangrove ecosystems. Further, mangrove ecosystems are increasingly impacted by changing global pressures, like climate warming and sea level rise (SLR), which can exacerbate the effects of nutrient pollution. We summarize the existing literature on nutrient enrichment influences on mangrove growth, reproduction, and mortality. We also review the impacts of excess nutrients on soil respiration, microbial communities and decomposition within mangrove ecosystems. Based on this literature, we identify three emergent implications of nutrient enrichment for mangroves: 1) resilience to extreme climatic events and SLR, 2) mangrove range expansion, and 3) carbon storage capacity. Lastly, we explore key gaps in the literature while offering future research suggestions to address them. We argue that understanding and addressing the impact of nutrient enrichment on mangrove ecosystems is crucial to protect their ability to mitigate and adapt to the challenges of climate change.

1. Introduction

The threat of nutrient enrichment has grown in coastal ecosystems over the past few decades (Downing et al., 1999; Cloern, 2001; Bricker et al., 2008). Nutrients can enter estuarine and marine ecosystems naturally through geological weathering and ocean upwelling (Bricker et al., 2008). Anthropogenic inputs of nitrogen (N) and phosphorus (P) from agriculture, aquaculture, wastewater treatment, urban runoff, and burning of fossil fuels, now exceed natural inputs worldwide (CENR, 2000, NRC, 2000). Nutrient enrichment has led to deadly blooms of phytoplankton and *Sargassum* (Paerl, 1997; Lapointe et al., 2020; 2021), coral reef deterioration (Hughes et al., 2003), and altered ecosystem functioning (Scheffer et al., 2001; Silbiger et al., 2018). As marine ecosystems continue to experience land use change, rising sea levels, altered weather patterns, and global warming, the threat of nutrient enrichment is predicted to intensify (Corredor et al., 1999; Kennish, 2002).

Coastal wetlands, such as salt marshes and mangroves, lie on the interface between marine and terrestrial habitats and mitigate nutrient loads for adjacent ecosystems like coral reefs and seagrasses (Clough et al., 1983; King and Lester, 1995). Mangrove wetlands can alleviate nutrient pollution through rapid nutrient uptake, long-term burial, or denitrification, thus protecting surrounding marine waters and organisms (Valiela and Cole, 2002). However, coastal wetlands themselves are still vulnerable to the impacts of nutrient enrichment. Excess nutrients have been implicated in a loss of soil shear strength and marsh structural integrity along creek edges, ultimately converting marshes to mudflats (Turner, 2011; Deegan et al., 2012). Further, following N enrichment, salt marshes slowed belowground organic matter (OM) accumulation rates—a process which allows for wetlands to keep pace with rising sea levels (Turner et al., 2009)—though the consequences of nutrient addition for marsh sustainability remain highly controversial (Morris et al., 2013). The impacts of nutrient enrichment have been heavily studied in temperate saltmarshes and may inform our understanding of nutrient impacts in mangrove wetlands.

Mangrove forests have historically been used as a wastewater treatment option for urban (Clough et al., 1983; Wong et al., 2007), agricultural, and aquacultural waste (Robertson and Phillips, 1995; Reef et al., 2010; Ouyang and Guo, 2016). Mangroves are a group of tropical and sub-tropical woody plants that have adapted to grow in various coastal and intertidal zones such as deltas, estuaries, and lagoons (Rovai et al., 2018). Like salt marshes, mangroves provide a wide array of important ecological services such as carbon (C) sequestration (Mcleod et al., 2011), coastal erosion protection (Marois and Mitsch, 2015), both

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physical and chemical buffering (Valiela and Cole, 2002; Singh et al., 2005), and habitat provision for key marine fish and bird species (Ewel et al., 1998; Kelleway et al., 2017). Although mangroves have been cited for their ability to act as nutrient sinks, due to high rates of nutrient uptake and denitrification, nutrient enrichment can have direct and indirect impacts on mangrove trees (Kaplan et al., 1979; Seitzinger, 1988).

Mangrove forests are among the most critically threatened ecosystems, and although mangrove deforestation has slowed in recent decades, mangrove forests have lost 25–35% of land area due to land use change and pollution (Valiela et al., 2001; Alongi et al., 2002; van Lavieren et al., 2012; Friess et al., 2019). Additionally, mangroves continue to be heavily impacted by nutrient runoff and subsequent enrichment. For example, mangrove ecosystems in Belize (Buck et al., 2019; Wells et al., 2019), Brazil (Queiroz et al., 2020), and India (Bala Krishna Prasad, 2012) have documented elevated nutrient levels due to the inefficient use of fertilizers, unregulated wastewater management practices, and contamination from aquaculture farms. Although mangrove restoration efforts have increased recently (Feller et al., 2017), it is important to understand mangrove vulnerability to the impacts of nutrient enrichment to better inform these efforts. In order to maintain natural and restored mangrove ecosystems and the vital services they provide, we must first understand the comprehensive impacts of nutrient enrichment on mangrove ecosystems. Previous reviews have discussed nutrient cycling and introduced the threat of nutrient enrichment, typically in coastal marshes (Singh et al., 2005; Turner et al., 2009; Reef et al., 2010; Morris et al., 2013, Mozdzer et al., 2020). Yet, no papers to our knowledge have compiled and connected the various impacts of nutrient enrichment on mangrove growth and belowground processes, such as decomposition and soil respiration. The aim of this review is to summarize the current literature addressing both the plant- and soil-mediated impacts of nutrient enrichment within mangrove ecosystems. We define plant-mediated impacts as nutrient enrichment effects that directly impact mangrove growth, mortality, primary productivity, and reproduction. Soil-mediated impacts are nutrient effects that have the potential to impact mangrove trees through alterations in soil respiration, microbial community dynamics, and decomposition rates within the soil.

In conducting the literature search for this review paper, we used key search terms including “mangroves,” “nutrient enrichment,” and a targeted response variable—“growth”, “reproduction”, “resiliency”, “soil respiration”, “microbial community” and “decomposition”. For the scope of this review, we only included studies with similar study designs that directly fertilized mangrove soils in either greenhouse or field environments in order to better compare mangrove responses to known nutrient enrichment (N, P, N + P, or N + P + K). We included 25 studies that fit this criteria for the plant and soil-mediated impact sections. It is important to note the geographical bias in the studies included in this review, with a predominant concentration in North and Central America, Asia, and Australia. While these aforementioned regions have been extensively studied, others have not and potential gaps in our understanding may exist for mangroves in both Africa and South America. These regions of the world collectively hold approximately half of the world’s mangrove area (Bunting et al., 2018) and our inequitable representation of nutrient effects on mangroves in South America and Africa may limit our conclusions. We also included some comparisons to coastal marshes where mangrove literature was lacking. Although marshes and mangrove ecosystems differ, some of the extensive work on marshes and nutrient enrichment may parallel impacts in mangrove ecosystems.

We first describe the limiting nutrients within mangrove ecosystems and provide a general overview of how nutrient scarcity limits mangrove productivity. We then examine how mangroves can be directly impacted by N, P, and potassium (K) enrichment through changing growth, reproductive output, and resiliency to extreme conditions, such as drought, hurricanes, freezes, and SLR. We then explore the soil-mediated effects of nutrient enrichment on mangroves such as changes in soil respiration, microbial communities, and decomposition. Lastly, we explore the emergent implications of nutrient enrichment on mangrove forests as wells as the ecosystem services they provide and offer future research suggestions.

2. Background

2.1. Key nutrients in mangrove ecosystems

Mangroves are adapted to live in anoxic and often nutrient-poor environments (Plaziat et al., 2001; Reef et al., 2010). Nutrients can enter a mangrove ecosystem from N fixation, atmospheric deposition (Alongi et al., 1992; Joye and Lee, 2004; Alongi, 2020), oceanic sources through upwelling, tidal pumping, and episodic flooding, as well as from terrestrial sources through upland-draining creeks (Singh et al., 2005; Reef et al., 2010). Similar to trees in terrestrial ecosystems, mangrove tree growth can be strongly impacted by available N or P (Feller et al., 2003a; Lovelock et al., 2007a). Within mangrove soils, microbial N processes—including denitrification, ammonification dissimilatory nitrate reduction to ammonium, (DNRA), and anaerobic ammonium oxidation (anammox)—form a complex microbial N transformation cycle (Fig. 1A, Reddy et al., 1983; Purvaja et al., 2008; Li et al., 2011). In wetland soils, N is typically recycled through DNRA from nitrate (NO_3^-) to generate ammonium (Fernandes et al., 2012; Cao et al., 2016; Luvizotto et al., 2019).

Ammonium (NH_4^+) is the most common form of mineral N within mangrove ecosystems (Alongi, 1994; Reef et al., 2010) and is readily available for uptake by mangrove roots in the soil (Holmboe and Kristensen, 2002). However, NH_4^+ and nitrite (NO_2^-), can be transformed into gaseous forms and released into the atmosphere through anammox and denitrification, respectively, which accounts for about 30–79% of N loss in marine environments (Trimmer and Nicholls, 2009; Li and Gu, 2011; Wang et al., 2015). Nitrate is another form of N that can be taken up and incorporated into tree biomass; however, due to high rates of denitrification in most wetland ecosystems, NO_3^- and NO_2^- pools are rapidly depleted compared to NH_4^+ (Alongi, 1994; Corredor and Morell, 1994). Although mangroves grown in greenhouse experiments can take up NO_3^- (Boto et al., 1985), various field experiments have concluded that NH_4^+ is the preferred N form for mangrove uptake (Smirnoff et al., 1984; Whigham et al., 2009; Reef et al., 2010).

Similar to other tropical forests (Tiessen, 2008), P cycling within mangrove ecosystems can be highly efficient, with an estimated 88% of the P pool being recycled due to highly efficient P resorption during leaf senescence (Boto and Bunt, 1982; Feller et al., 1999; Lovelock et al., 2007a). Although most P in mangrove soils occurs in organic pools, inorganic forms of P, such as phosphates, are most available for plant uptake (Boto, 1988). Most inorganic phosphates are bound to metals, such as calcium (Ca), aluminum (Al), and iron (Fe). In more oxygenated soil layers or microsites, typically in the rhizosphere, P can be bound as iron-phosphate ($FePO_4$). Within the rhizosphere, phosphate-solubilizing bacteria, as well as arbuscular mycorrhizal (AM) fungi, can solubilize $FePO_4$ (Fig. 1B), allowing for the uptake of P by mangrove roots (Vazquez et al., 2000; Singh et al., 2005; Reef et al., 2010). However, solubilization of phosphates can be inhibited in high saline environments (Sengupta and Chaudhuri, 2002). Inorganic forms of both P and N can also interact with negatively charged clay particles within soils (Fig. 1C) and can be exchanged and taken up by plants via cation exchange (Hogan et al., 2004, Steinmuller and Chambers, 2019).

Potassium (K) is another important macronutrient responsible for maintaining osmotic regulation in high saline environments (Downton, 1982; Reef et al., 2010). Although K is relatively high in seawater, sodium (Na) can interact competitively in the uptake of K by plants with increasing salinity (Ball et al., 1987). Potassium deficiency has been found to reduce photosynthetic capacity via diminished functional photosystem II in mangrove leaves (Ball et al., 1987). Yet, few studies

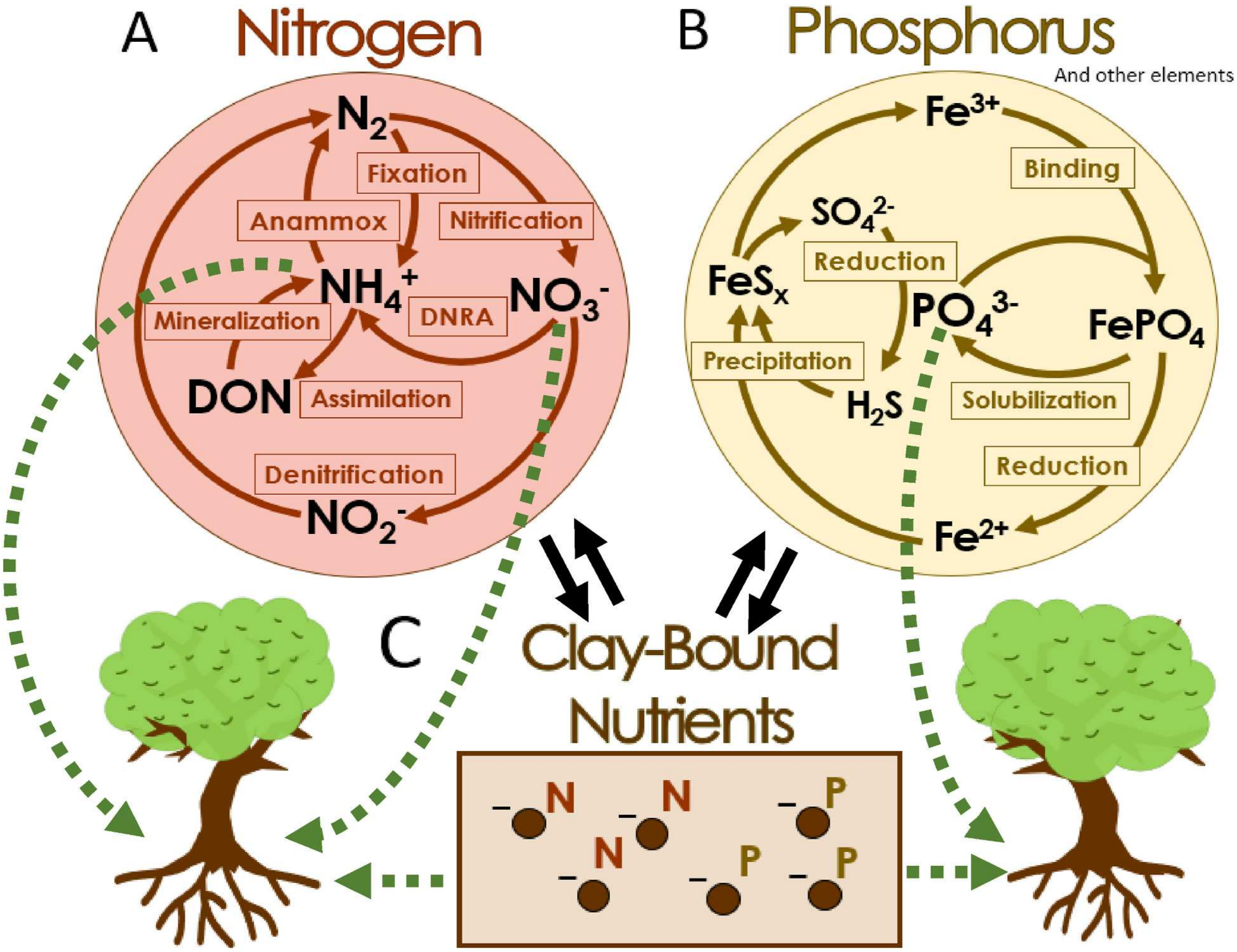

Fig. 1. Nutrient cycling dynamics of nitrogen (1 A) and phosphorous (1 B) in wetland ecosystems. Nutrient pools are labeled in black letters. Arrows represent pathways within and between nutrient cycles, soils, and plants. Some forms of inorganic N and P can interact with negatively charged clay particles (1C) that can be available via cation exchange.

have investigated the direct impact of K enrichment on mangrove growth, with only a few studies investigating the interacting effects between N, P and K availability using NPK fertilizers (Feller, 1995; Yates et al., 2002; Graham and Mendelssohn, 2016). Consequently, there have been very few findings indicating the K is a primary limiting nutrient for mangrove growth but that it may become limiting with the alleviation of primary limiting nutrients such as N and P (Reef et al., 2010). As a result, most studies have focused on using the macronutrients N and P in enrichment experiments. Other secondary macronutrients, including Mg^{2+} and Ca^{2+}, are important for regulating primary production and increasing salt tolerance (Cohen et al., 1999). These cations are relatively abundant in seawater, so they have not been studied as a limiting nutrient and are typically utilized to inform mangrove responses to N, P, N + P, or N + P + K enrichment (Reef et al., 2010; Alongi, 2021). There are varying abiotic factors that can determine the dominant nutrient that limits growth across and within a mangrove ecosystem.

2.2. Shifts in nutrient limitations across ecosystem gradients

Nitrogen and P limitation can vary considerably within a mangrove forest and can be influenced by inundation frequency (Lovelock et al., 2006), salinity stress (Feller et al., 2003b; Reef et al., 2010; Ahmed et al., 2022), latitude (McKee et al., 2002; Feller et al., 2013), and mangrove species (Feller et al., 2003b; Lovelock and Feller, 2003). Although nutrient limitation trends are complex, mangroves found in tropical or more inundated soils tend to be more P-limited while mangroves growing in sub-tropical or saline soils tend to be more N-limited (Feller et al., 2003a; Reef et al., 2010). Phosphorus has been implicated in water transport in mangrove tissues, which may be attributed to its importance in phosphorylation—the addition of a phosphate groups to a target molecule—that aid in regulating water channel functioning (Johansson et al., 1998; Lovelock et al., 2006). As a result, flood-related stress could increase P demand in plants due to more anoxic conditions inhibiting water uptake via roots (Greenway and Gibbs, 2003). Due to strong weathering and high rates of nutrient leaching in the tropical terrestrial soils, tropical mangrove forests are typically more P-limited than sub-tropical ecosystems (Boto and Wellington, 1983, Lovelock et al., 2007a). Continental tropical soils, the main terrestrial input for P in tropical lagoonal, delta, and estuarine mangrove ecosystems, are more P depleted and N can be replaced consistently in these systems through N-fixation (Reich and Oleksyn, 2004; Reef et al., 2010). For isolated mangroves found on islands, the concentrations of P in unpolluted seawater and porewater are low, likely due to a low influx of P from oceanic sources for fringing mangrove ecosystems (Alongi et al., 1992; Singh et al., 2005).

Salinity stress also has effects on nutrient limitations in mangroves. Available nutrients, such as NO_3^- and NH_4^+, typically decrease with increasing salinity levels, most likely due to reduced microbial activities within highly saline sediments (Alongi, 2020; Ahmed et al., 2022). Further, AM fungi can play an important role in the solubilization of metal bound phosphates for mangrove root uptake (Reef et al., 2010). Yet, AM fungi are typically found in higher concentrations at lower salinities—less than 11.2 psμ—which could reduce the take up of P by mangrove roots (Sengupta and Chaudhuri, 2002). In a wetland in Florida, dwarf *Avicennia germinans* in the hypersaline interior were more N limited than the fringing *Rhizophora mangle* (Feller et al., 2003b). Although primary nutrient limitation could be due to differences in mangrove species and nutrient uptake capacity (Lovelock and Feller, 2003), N demand could be higher in a hyper-saline environment due to the need for osmolytes. Many genera of mangroves have adapted to live in hypersaline environments by regulating salinity through the excretion of salts via osmoregulatory compounds, or osmolytes (Ahmed, 1992; Parida and Jha, 2010; Reef and Lovelock, 2015). Mangroves in the *Xylocarpus* genera utilize the amino acid, proline, while species in the *Avicennia* and *Heritiera* genera utilize methylated quaternary ammonium compounds (Parida and Jha, 2010, Popp et al., 1988). Nitrogen is an essential element in these osmolytes (Popp et al., 1988) and therefore, may increase the demand for N for mangroves in higher salinities (Feller et al., 2003b).

Box 1. Section Outline

Nutrient Dynamics in Mangrove Ecosystems
- Nitrogen and Phosphorous limited
- Nitrogen and Phosphorous highly conserved
- Inundation-stressed mangroves more P-limited
- Salinity-stressed mangroves more N-limited

Direct Nutrient Effects on Mangroves
- Above-ground growth
- Below-ground growth
- Reproductive Investment
- Resiliency to extreme events (drought, hurricanes, freezes)

Indirect Nutrient Effects on Mangroves
- Soil respiration
- Microbial biomass and diversity
- Decomposition Rates

Iron (Fe) also plays an important role in mangrove growth (Alongi, 2010) and organic C binding (Liu et al., 2021). Further, P dynamics and cycling are closely linked to the activation of Fe within mangrove ecosystems (Sherman et al., 1998; Singh et al., 2005). Iron enrichment led to enhanced growth of *Avicennia marina* seedlings in plots, in the only Fe-addition study in mangroves we could find (Almahasheer et al., 2016), suggesting that Fe enrichment and limitation still needs to be considered in additional field studies. Therefore, in this review, we will not be examining Fe as a main limiting nutrient of mangroves and focus on the literature from both N and P enrichment studies.

3. Plant-mediated impacts

3.1. *Aboveground growth*

One of the most common documented mangrove responses to nutrient enrichment is an increase in aboveground growth and biomass allocation to aboveground structures (Feller, 1995; Lovelock et al., 2007b; Hayes et al., 2017; Weaver and Armitage, 2020). For *A. germinans* in the Gulf of Mexico, USA, the addition of NPK fertilizer increased tree maximum height and overall size distributions. After two years, the total aboveground biomass—both woody and leaf tissues—of these same *A. germinans* shrubs were more than two times that of control shrubs (Weaver and Armitage, 2020). Similarly, for *A. germinans* in northeast Florida, USA, N addition increased tree height, shoot biomass, and canopy cover (Dangremond et al., 2020). These mangrove shrubs are specifically found near their poleward limit in a shifting marsh-mangrove ecotone (Cavanaugh et al., 2014; Saintilan et al., 2014). The competition with marsh grasses may allow for niche differentiation of nutrient uptake, potentially due to different rooting strategies or plant phenology (Dangremond et al., 2020).

Nitrogen-stimulated growth was also supported by a greenhouse experiment with *A. marina* in Australia, as high nutrient-treated seedlings were significantly taller than those in the low nutrient treatments (Hayes et al., 2017). Contrastingly, in a concurrent field N fertilization experiment, there was no difference in total plant biomass or in relative growth rate across the different nutrient treatments in mature *A. marina* trees, suggesting a stronger N influence on mangrove seedlings than mature trees (Hayes et al., 2017). However, N-stimulated growth occurred in dwarf *A. marina* trees in South Africa, as N and N + P enriched shrubs had greater heights, biomass, and branching compared to control and P enriched shrubs (Naidoo, 2009). These dwarf shrubs experienced hypersaline conditions of approximately 60 psμ which could have contributed to the clear N limitation (Naidoo, 2009). Similarly, for subtropical *A. germinans* in the saline shrub zone in Florida, N was more limiting than P (Feller et al., 2003b), indicating a greater demand for N in more saline environments for *Avicennia* shrubs. As discussed previously, mangroves in the *Avicennia* genera have adapted to regulate salt intake through osmolytes, typically N-based compounds (Parida and Jha, 2010, Popp et al., 1988).

Conversely, the addition of nutrients does not always stimulate mangrove productivity aboveground, as has been seen in other studies. For example, *Heritiera littoralis* seedlings in Tanzania did not respond to NPK fertilization (Mangora, 2016). Additionally, seedlings grown in the highest nutrient (NPK) and highest salinity treatment had reduced photosynthetic rate, suggesting a negative interaction on photosynthetic capacity between salinity and nutrient availability (Mangora, 2016). Conversely, for mature *A. germinans* shrubs in Florida, the addition of N allowed for greater net photosynthesis and accumulation of biomass (Lovelock and Feller, 2003), which could be attributed to a N-induced stimulation of Rubisco carboxylation—a key step in the photosynthetic production of sugars (Sturchio et al., 2022). Nitrogen has been implicated in the alleviation of water stress in mangroves, specifically in increasing water use efficiency (Martin et al., 2010). This enhancement in water use efficiency is especially beneficial for mangroves living in high salinity environments, aiding in greater gas exchange and photosynthetic capabilities (Krauss and Lovelock, 2022). Conversely, P demand on mangrove growth is typically influenced by inundation stress. Feller (1995) found that more inundated dwarf *R. mangle* shrubs in Belize responded to P enrichment but not to N. This finding was supported in a later study in Belize, as the more inundated, dwarf *R. mangle* shrubs responded more strongly to P while fringing *R. mangle* trees were more N limited, which the authors attributed to differences in tidal flushing and nutrient exchange rather than salinity (Feller et al., 2003a). Although differences in nutrient limitation and mangrove growth responses to added nutrients depend on local nutrient regimes, edaphic conditions, climate, and abiotic stressors, mangroves often increase allocation in aboveground biomass in response to nutrient enrichment.

3.2. *Belowground biomass allocation*

Belowground biomass allocation also aids mangroves in maintaining elevation with respect to SLR, yet belowground responses to nutrient enrichment have been poorly characterized in mangroves (Cahoon et al., 2021). Following the resource-ratio hypothesis, it is expected that as availability of nutrients increases, plants should invest proportionally fewer resources into belowground biomass in favor of aboveground growth, therefore decreasing the root-to-shoot (R:S) ratio (Tilman, 1991 and 1991, Lambers and Poorter, 1999; Reef et al., 2010).

In an *A. germinans* N-fertilization experiment in Texas, USA both above- and belowground biomass increased in N-treated trees, with a greater production of coarse roots rather than fine roots (Weaver and Armitage, 2020). Coarse roots (>2 mm) are larger than fine roots (<2 mm) and could have contributed to the significant increase in belowground biomass. The increase in belowground biomass was only attributed to the top 5 cm of the soil, indicating stimulation of shallower roots. In a greenhouse experiment, *A. marina* seedlings reduced R:S ratios in response to N + P fertilizer (Hayes et al., 2017). Similarly, the addition of N shifted R:S ratios of dwarf *A. marina* trees from 1.8:1 in control and P-fertilized trees to 0.8:1 in N and N + P treated trees in Africa (Naidoo, 2009). In New Zealand and Australia, the addition of N reduced belowground growth of *A. marina* trees in favor for more growth allocated aboveground (Lovelock et al., 2009). This reduction in R:S ratios led to enhanced aboveground growth rates but increased vulnerability to biotic and abiotic stressors, specifically drought and higher salinity (Lovelock et al., 2009). As different mangrove root structures are important for different functions, such as nutrient foraging (fine roots) and structural support and oxygen delivery (cable and prop roots and pneumatophores), nutrient influences on root allocation may produce varied plant growth outcomes (Srikanth et al., 2016).

Nutrient-induced changes in belowground growth have been extensively studied in coastal marshes, but the results often appear contradictory. For instance, root productivity may increase with added N while standing root biomass decreases (Graham and Mendelssohn, 2014), suggesting an increased root turnover rate. Across mangrove nutrient enrichment studies, one common finding is that belowground growth declines in proportion to aboveground growth (Lovelock et al., 2009; Naidoo, 2009; Hayes et al., 2017; Weaver and Armitage, 2020) (see Table 1). These changes in allocation have implications for C storage within mangrove ecosystems, as belowground biomass decreases with nutrient enrichment, leading to lower long-term C storage. Investigations of C allocation in mangrove forests suggest disproportionate C storage in belowground biomass (Komiyama et al., 2008; Khan et al., 2009; Ray et al., 2011) due to inundated soils with low decomposition rates (Lovelock, 2008; Ren et al., 2010). For example *R. mangle* forests in Belize, Panama, and Honduras are a main sources of OM accumulation and mangrove blue carbon (McKee et al., 2007) through the deep accumulation of mangrove peat (McKee and Faulkner, 2000). However, a mangrove forest that has been enriched with excess nutrients could reduce belowground growth allocation, which could lead to lower OM C storage within live roots, lower deposition of dead roots, and higher C turnover rates via aboveground respiration (Clough et al., 1997; Alongi, 2012; Hayes et al., 2017).

Mangroves are crucial for combating coastal erosion as mangrove trees are more efficient in coastal protection than any other wetland plant species (Doughty et al., 2017; Pennings et al., 2021). In general, mangroves increase soil shear strength with higher levels of belowground biomass (Wilson et al., 2012; Cahoon et al., 2020). If mangrove trees were to diminish root growth allocation, especially in fine roots, we could expect higher levels of coastal erosion in areas with high nutrient enrichment, leading to reduction of structural integrity of the soil and loss of wetland species. For example, Simpson et al. (2021) found that long-term N and P enrichment from bird guano deposition resulted in a progressive decline in island size of the Twin Cays off the coast of Belize. The mangrove islands that experienced roughly 15 years of natural eutrophication lost 51 ± 16% of the total island area compared to the 4 ± 1% area loss of control islands. The authors attributed the loss of peat-based mangrove clays to accelerated decomposition and loss of soil OM following chronic enrichment. This trend of

Table 1
Summary of mangrove-mediated impacts to fertilization. Response metrics are confined to the metrics included in this review. The stars indicate several sites within one study and include the general direction of the response metric.

Location	Site	Mangrove Species	Nutrient Treatment	Response Metric(s)	Direction of Response	Reference
Twin Cays, Belize	Smithsonian Institution's National Museum of Natural History Field Station	*R. mangle*	NH_4 (45:0:0; N:P:K) or P_2O_5 (0:45:0) or NH_4: P_20_5:K_20 (10:15:15)	Aboveground growth Reproductive investment	Increased	Feller (1995)
Twin Cays, Belize	Smithsonian Institution's National Museum of Natural History Field Station	*R. mangle*	Urea (45:0:0; N:P:K) or P_2O_5 (0:45:0)	Aboveground growth	Increased	Feller et al., 2003a
Florida, USA	Mosquito Impoundment 23 at Indian River Lagoon	*R. mangle, A. germinans*	Urea (45:0:0; N:P:K) or P_2O_5 (0:45:0)	Aboveground growth	Increased	Feller et al., 2003b
Bocas del Toro, Panamá	Isla San Cristóbal	*R. mangle*	Urea (45:0:0; N:P:K)	Aboveground growth	Increased	Lovelock and Feller, 2003
New Zealand*	Waikopua and Whangapoua estuaries	*A. marina*	Urea (45:0:0; N:P:K)	Aboveground growth	Increased	Lovelock et al. (2009)
Durban, Africa	Richards Bay Harbour	*A. marina* seedlings	Urea (45:0:0; N:P:K) and/or P_2O_5 (0:45:0)	Aboveground growth Belowground growth	Increased Decreased	Naidoo, 2009
Zanzibar, Tanzania	Ruvu River Estuary	*H. littoralis* seedlings	Granular farm fertilizer (20:20:20; N:P:K)	Aboveground growth Belowground growth	No change No change	Mangora, 2016
Moreton Bay, Australia	Tinchi Tamba Wetland Reserve	*A. marina*	Urea (45:0:0; N:P:K) or P_2O_5 (0:45:0)	Aboveground growth Belowground growth	No change No change	Hayes et al. (2017)
	Greenhouse Experiment	*A. marina seedlings*			Increased Decreased	
Texas, USA	Port Aransas	*A. germinans*	Osmocote all-purpose landscape fertilizer (19:6:12; N:P:K)	Aboveground growth Belowground growth	Increased	Weaver and Armitage (2018)/(2020)
Florida, USA	Guana Tolomato Matanzas National Estuarine Research Reserve	*A. germinans*	4.95 M NH_4^+ nitrate (NH_4NO_3) solution	Aboveground growth Reproductive investment	Increased	Dangremond et al. (2020)
New Zealand and Australia*	Several sites[1]	*R. mangle, A. germinans, A. marina, R. lamarckii, C. tagal, L. racemosa*	Urea (45:0:0; N:P:K) or $Ca(H_2PO_4)_2$	Resiliency/Mortality	Reduced resiliency to drought	Lovelock et al. (2009)
Florida, USA	Mosquito Impoundment 23 at Indian River Lagoon	*R. mangle, A. germinans*	Urea (45:0:0; N:P:K) or P_2O_5 (0:45:0	Resiliency/Mortality	Reduced resiliency to hurricane	Feller et al. (2015)
Florida, USA	Guana Tolomato Matanzas National Estuarine Research Reserve	*A. germinans*	NH_4 (45:0:0; N:P:K) or P_2O_5 (0:45:0)	Resiliency/Mortality	Enhanced resiliency to freeze events	Feller et al. (2022)

nutrient-induced erosion has also been well documented in saltmarshes, with both a loss of soil shear strength and marsh structural integrity following fertilization (Turner, 2011; Deegan et al., 2012). Coastal eutrophication can reduce ecosystem stability by contributing to accelerated loss of wetlands and mangrove islands, with potential consequences for C storage and mangrove resilience to environmental variability with climate change.

3.3. Reproductive investment and success

Reproductive output of mangroves can be a key indicator of establishment success, community growth, and mangrove expansion (Por and Tomlinson, 1987; Sousa et al., 2003; Devaney et al., 2017). For plants, the production of reproductive organs and fruits is energetically costly and reproductive investment may be lowered in times of high stress or low nutrient availability (Obeso, 2002). Many mangrove genera reproduce viviparously and supply growing propagules with nutrients and carbohydrates (Alleman and Hester, 2011). These propagules are the unit of dispersal for mangrove trees and can provide indication of resource investment strategy from parents to offspring (Tomlinson, 2016). Nutrient influences on mangrove reproductive investment and resultant seedling success have not been synthesized.

For unfertilized dwarf *R. mangle* trees in Belize, reproductive investment and success are low, with few flowering branches and small, deformed propagules (Feller, 1995). Following P enrichment, these dwarf *R. mangle* trees significantly increased the number of flowering shoots and seven out of twelve P-enriched trees had buds or propagules compared to only one of the twelve control trees (Feller, 1995). Similarly, Dangremond et al. (2020) found that reproductive output increased with the addition of N for mature *A. germinans* shrubs at their latitudinal limit. Not only did the number of flowers triple in the N treatments, but also reproductive branches had significantly more biomass devoted to propagules. Results from this study demonstrated that N enrichment increased mangrove growth rates, cover, and reproductive allocation (Dangremond et al., 2020). Within this same study, saltmarsh grass cover decreased in fertilized mangrove plots, indicating that fertilized mangroves were able to more rapidly outgrow and overtop neighboring marsh grass species (Dangremond et al., 2020). These increases in reproductive investment coupled with increased clonal growth and freeze tolerance (Feller et al., 2022) suggest that increased N availability could accelerate encroachment and competition of mangroves into saltmarshes that previously dominated in this ecotonal zone.

Furthermore, mangrove seedling establishment success in transitioning marsh-mangrove ecotones may also be impacted by nutrient enrichment. Mangrove seedlings have successfully established further poleward with warming global temperatures and increasing sediments and sea levels (Cavanaugh et al., 2014, 2015; Rogers et al., 2005; Saintilan et al., 2014). Not only does seedling establishment depend on temperature, but establishment success may also be nutrient limited (Krauss et al., 2008; Qin et al., 2020). For *Bruguiera sexangula* seedlings, N enrichment

Led to greater seedling survival and growth, although this came at a cost to seedling root growth (Gillis et al., 2019). With increased nutrient availability, propagules and seedlings may be more successful in encroaching into established wetland ecosystems, therefore further expanding the range of mangrove-dominated ecosystems (Dangremond et al., 2020).

3.4. Mortality and resilience

Although many studies have indicated increased aboveground biomass in nutrient enriched mangroves, few studies have investigated the corresponding resilience of fertilized mangrove trees (see Table 1). Lovelock et al. (2009) found an increase in tree mortality, especially for fringe mangrove forests, in response to various nutrient treatments. This increase in mortality was seen in tandem with an increase in salinity and decrease in precipitation, leading to the conclusion that nutrient enriched mangrove ecosystems may be less resilient to drought. Although these findings have only been reported in one study, the implications of this research could indicate a larger trend of fertilized mangroves having lower resilience to drought and increased salinity.

Another measure of coastal ecosystem resilience is growth responses after big storm events. Castañeda-Moya et al. (2020) found that Hurricane Irma provided a large P subsidy to a mangrove ecosystem in the Florida Everglades and that the mangroves exhibited higher foliar P concentrations following this event. Conversely, the addition of nutrients has been found to amplify the detrimental impacts of hurricanes on mangrove canopy and recovery (Feller et al., 2015). Typically, larger mangrove trees usually sustain greater damage after a hurricane (Vogt et al., 2012), as more low-stature (shrubs) mangroves are inundated during a hurricane event and can avoid the intense winds and wave surges (Craighead, 1971). After eight years of fertilization, *A. germinans* shrubs in Florida were heavily impacted by two consecutive hurricanes with greater canopy loss and reduced recovery than the unfertilized plants, which were smaller (Feller et al., 2015). Similar to other tree species with lower R:S ratios, more aerial drag on the canopy of mangroves in high nutrient environments, coupled with less anchorage by roots, may exacerbate damage and compromise recovery and growth after big storm events.

For mangroves growing at their northern range limit, freeze event responses are another key indicator of mangrove resilience, as deep freeze events can lead to large mangrove die-offs (Cavanaugh et al., 2014; Cook-Patton et al., 2015). Conversely to findings for hurricane resilience following enrichment, excess N can bolster *A. germinans* resiliency to freeze events in marsh-mangrove ecotones (Feller et al., 2022). Not only were fertilized mangrove trees more resilient to freeze events, but they also more readily took up nutrients than adjacent grasses (Feller et al., 2022). This decreased mortality due to freezes may indicate that wetlands with high nutrient enrichment that are in the preliminary stages of mangrove encroachment may be more likely to transition from marsh-to mangrove-dominated vegetation. Additional studies investigating the resiliency of enriched mangroves to varying environmental stressors, such as drought, elevated salinity, freeze events, hurricanes, and SLR are needed across mangrove species and forest types.

4. Soil-mediated impacts

4.1. Soil respiration

Mangrove forests are large C sinks worldwide, mainly due to low soil respiration while maintaining high rates of productivity (Chmura et al., 2003; Lovelock, 2008; Donato et al., 2011; Alongi, 2014). In terrestrial ecosystems, soil respiration can be highly influenced by nutrient availability, thus altering net primary production and growth allocation of roots (Raich and Nadelhoffer, 1989; Tang et al., 2005). In temperate coastal marshes, soil respiration has been found to increase with greater nutrient availability (Morris and Bradley, 1999). For mangrove soils, nutrient enrichment had variable effects on root respiration across mangrove forest types (Lovelock et al., 2014). In transitional and scrub forests, N- and P- enriched plots had as much as 86.5% and 72.8% greater soil respiration, respectively, compared to control plots. However, this stimulation was only seen minimally in fringing and landward forests. The authors indicated that this difference in response to nutrient enrichment could be due to differences in nutrient limitations across forest types or due to differences in salinity, as the responsiveness in soil respiration was found to decline with increasing salinity. Across sites in both the tropics and subtropics, nutrient enrichment increased soil respiration by roughly 25% in scrub, transitional, and fringing mangrove forests (Lovelock et al., 2014). These findings may indicate that nutrient enrichment has the potential to alter C cycling within mangrove ecosystems.

Additionally, P-enriched *R. mangle* shrubs in Twin Cays, Belize, had higher root and overall soil respiration than unfertilized scrub and fringe trees (Lovelock et al., 2015). Although fertilized *R. mangle* plants had higher gross primary productivity, there was reduced proportion of C burial following enrichment compared to control trees (Lovelock et al., 2015). Alteration of soil C stocks has been documented in enriched mangrove ecosystems with a 23% reduction of stored organic C in surface soil C stocks compared to control plots, thus leading to reduced soil carbon-to-nitrogen (C:N) ratios (Palacios et al., 2021). However, the C flux within mangrove ecosystems was not significantly affected by enrichment (Palacios et al., 2021).

Although C accumulates in most tidal wetlands—as C inputs typically exceed C losses—the addition of nutrients could stimulate C losses (Smith et al., 1983). Additionally, added nutrients could have a larger absolute effects on productivity as it often exceeds C lost to respiration or decomposition (Kirwan and Blum, 2011). Global syntheses of mangrove C stocks are increasingly refined (Donato et al., 2011; Sanderman et al., 2018; Kauffman et al., 2020), but may not predict nutrient-induced changes in C cycling. Though altered soil respiration in response to nutrients has only been documented in a few studies, these findings could suggest a larger trend of nutrient enrichment impacts on C sequestration in mangrove ecosystems.

4.2. *Microbial functioning*

Mangrove trees depend on mutually beneficial interactions with microbial communities, specifically microbes that reside in and near the roots to aid in the uptake and cycling of nutrients (Thatoi et al., 2013; Xu et al., 2018; Liu et al., 2020). Mangrove ecosystems can host highly diverse microbial communities, mainly bacteria and fungi, that conduct essential functions such as nutrient cycling, N fixation, and C flux processing (McKee, 1993; Holguin et al., 2001; Thatoi et al., 2013). Like mangroves, microbes are affected by changes within the ecosystem, including increased availability of nutrients (Singh et al., 2005; Keuskamp et al., 2015a) and dominant species changes (Barreto et al., 2018).

Although highly debated, soil microbial functioning has been associated with microbial biodiversity, specifically with keystone microbial species (Krause et al., 2014; Yang et al., 2021). Several studies have found that nutrient enrichment, specifically N, leads to a reduction in overall soil microbial biodiversity and community composition in mangrove ecosystems (Wang et al., 2018; Craig et al., 2021; Palacios et al., 2021). Craig et al. (2021) specifically observed dramatic changes following N fertilization in soil microbial composition with decreased abundances of sulfate-reducing bacteria. This decrease in sulfate-reducing bacteria could alter overall soil microbial functioning as these bacteria are key components in anoxic mineralization of OM and anthropogenic pollutants (Yuan and Chang, 2007; Lyimo et al., 2009). Palacios et al. (2021) saw similar decreases in soil microbial diversity in response to N and P addition, with an increase in abundance of ammonium-oxidizing archaea, which are integral components of N cycling in the oxidation of ammonia to produce nonreactive atmospheric nitrogen (N_2) gas (Wang et al., 2013). This growth in anammox bacteria could result in changes of N cycling with a depletion in the NH_4^+ pool and a subsequent increase in the production of N_2 gas and return to the atmosphere. Although soil microbial functioning can be carried out by redundant microbial species, understanding shifts in diversity of key microbial communities could provide insights into potential shifts in nutrient and other biogeochemical cycling in mangrove sediments.

Along with shifts in microbial diversity and community composition, microbial biomass can also be modified by nutrient enrichment. Keuskamp et al. (2015a) found that added N and P decreased soil microbial biomass in a fringing *R. mangle* forest in Belize. However, only added N, not P, decreased soil microbial biomass in P-limited dwarf *R. mangle* stand (Keuskamp et al., 2015a). Although it is relatively unknown how alterations in soil microbial biomass may impact microbial functioning, the accumulation of microbes is an important C sink in wetland soils (Holguin et al., 2001; Alongi, 2014). The reduction of microbial biomass following nutrient enrichment could lead to a reduction in the microbial C pool, as has been seen in a tropical marsh (Corstanje et al., 2007). Further, soil microbial biomass is a primary nutrient source in typical nutrient-poor ecosystems, such as mangrove wetlands (Singh, 2015a, 2015b; Vimal et al., 2017; Singh and Gupta, 2018). As mangrove ecosystems experience eutrophication events, the loss of soil microbial biomass could result in a subsequent altered nutrient turnover and availability for mangrove plants (Treseder, 2008). Changes in soil respiration have also been associated with changes in microbial biomass, which can be altered by increased nutrient availability. Soil microbial communities are fundamentally altered by nutrient enrichment which has the potential to alter microbial functioning implicated in ecosystem fluxes, such as nutrient cycling, soil respiration and decomposition (Holguin et al., 2001; Craig et al., 2021).

4.3. *Decomposition rates*

Decomposition rates can vary due to many factors including climate, oxygen availability, mangrove species, and litter quality (Huxham et al., 2010; Keuskamp et al., 2015b; Hayes et al., 2017; Chapman et al., 2019, Simpson et al., 2023). The rate of soil OM decomposition also typically corresponds with nutrient availability in both terrestrial and wetland ecosystems, although decomposition dynamics are difficult to unravel (Cebrián et al., 1998; Keuskamp et al., 2015b). Furthermore, studies vary with regards to the substrate used in decomposition analysis, with some using the tea bag index (Keuskamp et al., 2013; Hayes et al., 2017; Palacios et al., 2021) and others using leaf (Simpson et al., 2020; Yang et al., 2018) or root matter (Huxham et al., 2010; Simpson et al., 2020). Hayes et al. (2017) found that decomposition rates of tea leaves were higher in *A. marina* plots treated with N, although this was not seen across all mangrove forest types, such as the fringing mangrove forest. In Australia, decomposition followed a similar trend in *A. marina* plots, with greater decomposition rates of tea leaves in N + P treated mangrove plots (Palacios et al., 2021). Similarly, in a mesocosm experiment, added N stimulated the decomposition of *B. gymnorhiza* leaf litter (Yang et al., 2018). Additionally, the N-rich *A. marina* leaf litter exhibited greater decomposition rates compared to the *B. gymnorhiza* leaves with lower N content (Yang et al., 2018). Some effects of N enrichment on leaf litter decomposition were short-lived, with decomposition of enriched *A. germinans* leaf litter only accelerating in the first two months (Simpson et al., 2020).

Decomposition of mangrove roots occurs more slowly than that of labile leaf material, (Simpson et al., 2020), allowing for long-term C storage (Spivak et al., 2019). As a result, nutrient-induced changes in root decomposition could have a larger impact on C accumulation in mangrove ecosystems. In a field experiment in a mixed mangrove forest in Kenya, N enrichment had a positive effect on root decomposition rates for *B. gymnorhiza* roots (Huxham et al., 2010) (see Table 2).

The mangrove roots grown in N-enriched soils had lower C:N ratios and higher N content compared to unenriched root litter, which could attribute to the accelerated decomposition rates (Huxham et al., 2010). Furthermore, *A. marina* root litter, which had low C:N ratios, had the highest decomposition rates out of the three mangrove species (*A. marina*, *B. gymnorhiza*, *Ceriops tagal*), indicating a strong relationship between N content of litter and decomposition rate (Huxham et al., 2010).

In upland ecosystems eutrophication can lead to priming of OM processing because microbes can be N limited (Bei et al., 2022). In wetlands, OM decomposition is most often limited by oxygen (Chapman et al., 2019). Due to low oxygen, decomposition rates are slow, allowing for the accumulation of OM and aiding in vertical accretion and elevation gain relative to SLR (Callaway et al., 1996). Decomposition is also an important component of the C cycle in mangrove ecosystems as it is a major pathway of C loss (Simpson et al., 2020). However, nutrient enrichment has the capability to alter the quality and composition of soil

Table 2

Summary of soil-mediated impacts to fertilization. Response metrics are confined to the metrics included in this review. One star indicates an increase in decomposition of enriched *B. gymnorhiza* roots, and two stars indicates accelerated decomposition in the first two months but no difference after the conclusion of the 6 month study.

Location	Site	Predominant Mangrove Species	Type of Experiment	Nutrient Treatment	Response Metric(s)	Direction of Response	Reference
Belize, Panama, Florida (USA), Australia, New Zealand	Several sites[1]	*A. germinans, R. mangle, C. autralis, Rhizophora x lamarkii, A. marina*	Field	Urea (45:0:0; N:P:K) or P_2O_5 (0:45:0)	Soil Respiration	Increased	Lovelock et al. (2004)
Twin Cays, Belize	Lagoon of the Meso-American Barrier Reef	*R. mangle*	Field	Urea (45:0:0; N:P:K) or P_2O_5 (0:45:0)	Soil Respiration	Increased	Lovelock et al. (2015)
Twin Cays, Belize	Smithsonian Institution's National Museum of Natural History Field Station	R. mangle	Mesocosm	NH_4 (45:0:0; N:P:K) or P_2O_5 (0:45:0) or NH_4: P_2O_5:K_2O (10:15:15)	Microbial Biomass	Decreased	Keuskamp et al. (2015a)
Florida, USA	Guana Tolomato Matanzas National Estuarine Research Reserve	*A. germinans*	Mesocosm	N (NH_4NO_3) or P + K (KH_2PO_4) or N + P + K ($NH_4NO_3 + KH_2PO_4$)	Microbial Biomass Microbial Diversity	Decreased	Craig et al. (2021)
New South Wales, Australia	Towra Point Nature Reserve	*A. marina*	Field; Tea Bag Index	Scotts™ Fertilizer: (21.2:1.9:5.7; N:P:K)	Microbial Diversity Decomposition	Decreased No change	Palacios et al. (2021)
Mombasa, Kenya	Gazi Bay	*A. marina, C. tagal*	Field; Fertilized root matter	'Vitax' N (20% NH_3N) and P (17% P_2O_5)	Decomposition	Increased*	Huxham et al. (2010)
Moreton Bay, Australia	Tinchi Tamba Wetland Reserve	*A. marina*	Field; Tea Bag Index	Urea (45:0:0; N:P:K) or P2O5 (0:45:0)	Decomposition	Increased	Hayes et al. (2017)
Guangdong Province, China	Tsinghua University Shenzhen Graduate School	*A. marina, B. gymnorrhiza*	Mesocosm; Leaf matter	20 mg L^{-1} NH_4 + and 5 mg L^{-1} NO_3^-	Decomposition	Increased	Yang et al. (2018)
Florida, USA	Guana Tolomato Matanzas National Estuarine Research Reserve	*A. germinans*	Field; Fertilized leaf matter and root matter	NH_4 (45:0:0; N:P:K) or P_2O_5 (0:45:0)	Decomposition	No change**	Simpson et al. (2020)

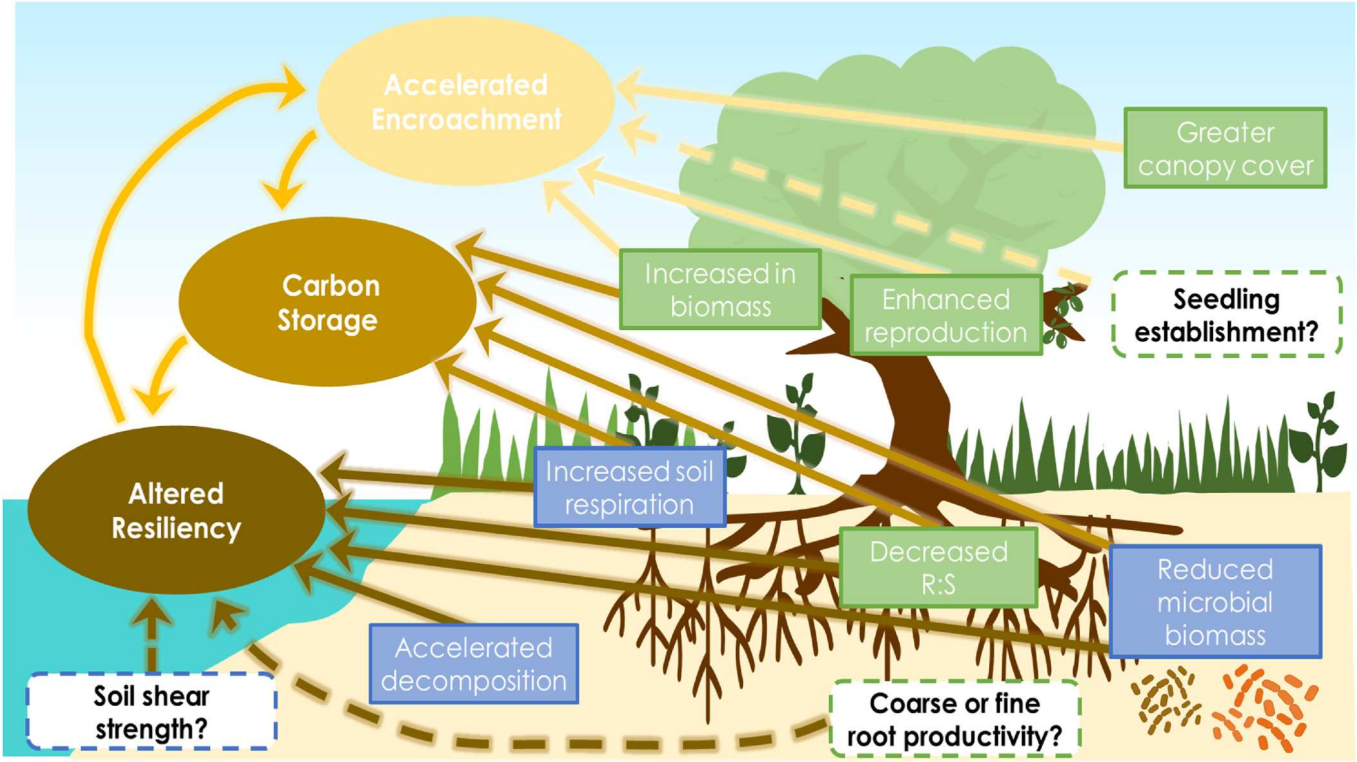

Fig. 2. Comprehensive impacts and implications of nutrient enrichment on mangrove systems. Colored boxes indicate individual responses summarized from previous studies, with green symbolizing mangrove-mediated impacts and blue is soil-mediated impacts. Solid arrows represent affiliation of findings to emergent implications shown as circles. Dotted arrows represent uncertainty of potential impacts that warrant future research questions, shown in white boxes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

OM by increasing N content of decomposing litter and thus potentially increasing decomposition in mangrove soils.

5. Emergent implications

The total impact of nutrient enrichment on coastal wetlands, especially mangroves, is highly controversial and remains unclear (Macreadie et al., 2017). We aimed to describe nutrient cycling and nutrient limitations within mangrove ecosystems and connect both the direct and indirect impacts of nutrient enrichment on mangroves. Across several studies, there are three prevailing emergent implications: modified mangrove resilience, accelerated encroachment, and altered carbon storage (see Fig. 2). We address each of these three implications below.

Mangroves have adapted to inhabit environmentally extreme conditions including high salinity, frequent flooding, nutrient scarcity, anoxic soils, and severe storm surges (Naskar and Palit, 2015). As a result, mangrove trees allocate a disproportionate amount of growth belowground (Burchett et al., 1984; Ball, 1988, 1997). Nutrient enrichment has been found to decrease growth allocation from roots to shoots and could therefore affect mangrove resiliency to extreme disturbances, such as drought and high salinity levels (Lovelock et al., 2009; Naidoo, 2009; Hayes et al., 2017; Weaver and Armitage, 2020). Extensive mangrove roots also provide anchorage to protect against damage from high winds and waves (Por and Tomlinson, 1987). If a mangrove ecosystem were to be enriched with nutrients, decreased allocation to individual tree roots could lead to higher mortality after severe storm events (Feller et al., 2015) and an overall decrease in coastal protection, although this possibly warrants further study. However, mangrove resilience to freeze events increased in marsh-mangrove ecotones, suggesting nutrient enrichment may increase mangrove resilience to certain disturbances, such as freezing (Weaver and Armitage, 2018; Dangremond et al., 2020; Feller et al., 2022), but not others, such as storms, drought, and high salinity (Lovelock et al., 2009).

Typically, mangrove ranges are limited due to winter freezes along established saltmarsh-mangrove ecotones. However, owing to warmer temperatures, altered precipitation patterns, and accelerating SLR, mangroves have migrated into predominantly saltmarsh ecosystems on five continents (Eslami-Andargoli et al., 2009; Cavanaugh et al., 2014; Armitage et al., 2015). Not only can nutrient enrichment aid in the establishment and success of encroaching mangrove seedlings, but it can also increase reproductive output, further advancing mangrove encroachment (Feller, 1995; Dangremond et al., 2020; Weaver and Armitage, 2020). As some areas continue to lose mangrove area due to nutrient enrichment, some areas may see expansion of mangrove into other wetland ecosystems.

Mangrove forests, along with other coastal ecosystems, are among the most efficient C sinks worldwide (Serrano et al., 2019). Not only do mangroves sequester great amounts of C, but decomposition and soil respiration are significantly lower than other terrestrial ecosystems (Cebrián et al., 1998, Jennerjahn and Ittekkot, 2002; Lovelock, 2008; Alongi, 2014). When enriched with N, mangrove soils have higher soil respiration and higher decomposition rates (Huxham et al., 2010; Lovelock et al., 2014; Hayes et al., 2017). Alterations in C burial in enriched mangroves could have implications in C cycling and global C budgets as N + P fertilization led to a reduction of C:N ratios and soil surface C stocks in (Palacios et al., 2021). Furthermore, it is possible that the addition of nutrients could have a direct influence on the composition of OM and thus decomposition rates of that OM in mangrove soils, as has been suggested for other wetlands (Sundareshwar et al., 2003; Wigand et al., 2009). For example, nutrient enrichment can lead to a reduction in root productivity relative to aboveground growth, which could lead to a reduction of root-derived OM and an increase in more labile leaf litter. Not only could this alteration in OM composition result in lower sedimentary C and soil C:N (Palacios et al., 2021; Chynel et al., 2022), but could also decrease the potential for long-term C storage of root-derived OM while increasing C loss via soil respiration (Spivak et al., 2019). As a result, enriched mangrove forests could increase C turnover and decrease long-term organic C storage, turning these ecosystems from C sinks to C sources.

6. Research recommendations

Throughout this review, gaps in the literature have become increasingly clear. Although some studies have investigated either mangrove- or soil-mediated impacts of nutrient enrichment, very few have looked into how nutrient enrichment can impact mangrove resiliency, encroachment, and C storage. Future studies should investigate how nutrient enrichment can aid in mangrove encroachment into saltmarshes by addressing seedling success within an enriched system and the morphological mechanisms that increase resiliency of mangroves to freeze events (e.g. Dangremond et al., 2020; Feller et al., 2022). Very few studies have investigated changes in fertilized mangrove resilience to drought, storm damage, or wave surges and should be investigated. Although some studies have found a loss of soil integrity in fertilized marshes (Turner, 2011; Deegan et al., 2012), no studies, to our knowledge, have investigated changes on soil integrity or soil shear strength in enriched mangrove ecosystems. Further, it is unknown how mangroves that grow along edges of wetlands may be impacted by nutrient enrichment, as mangroves could follow a similar trend of reduced creek bank structure found in saltmarshes (Deegan et al., 2012). Although Weaver and Armitage (2020) found significantly more coarse roots in fertilized mangrove trees, more studies are needed to investigate whether this trend could lead to lower soil shear strength.

It is important to note that although mangrove and marsh plant species share similarities, there are key differences in morphology, physiology, and climate and their respective response to nutrient enrichment may differ. For example, mangroves grow in warmer climates that tend to be more nutrient limited than more temperate marshes (Lovelock et al., 2007a; Mitsch and Gosselink, 2007). Not only are these tropical ecosystems potentially more sensitive to nutrient enrichment, but also the frequency of hurricanes in the tropics and subtropics could further exacerbate the impacts of nutrient enrichment. For example, as nutrient enrichment increases aboveground growth and reduces mangrove R:S, mangroves could be more top-heavy and less anchored, becoming more susceptible to damage or toppling via strong winds and wave action, as seen in Feller et al. (2015).

Additionally, no studies have examined how microbial reductions of key soil microbial communities—in either biodiversity or biomass—may affect overall microbial functioning and thus impact mangrove trees following enrichment. Alterations in soil microbial community functioning within mangrove ecosystems could lead to lowered mangrove resiliency to anthropogenic pollutants and disturbances, although this would need to be studied within mangrove ecosystems (Yang et al., 2021). No studies, to our knowledge, have investigated the impact of nutrient enrichment on fungal networks in mangrove forests, which have been shown to decrease in activity in terrestrial systems following nutrient enrichment (Bääth et al., 1981). Only recent studies have begun to investigate the impact of nutrient enrichment on C sequestration and storage in mangrove ecosystems (Palacios et al., 2021). More studies are needed to examine whether nutrient enrichment could lower long-term C storage as a result of decreased soil microbial biomass, as well as increased decomposition and soil respiration. Additionally, a study is needed to parse differences between respiration of mangrove roots (autotrophic respiration) and microbes (heterotrophic respiration) as each may respond differently to nutrient enrichment.

7. Conclusions

Nutrient eutrophication in estuaries is leading to organismal and ecosystem collapse around the world (Scheffer et al., 2001; Hughes et al., 2003; Silbiger et al., 2018, Lapointe et al., 2020). Although mangroves can be effective nutrient sinks (Valiela and Cole, 2002) and thus benefit adjacent reefs, seagrasses, and other marine ecosystem, we show that mangrove forests are vulnerable to anthropogenic nutrient enrichment via both plant-mediated and soil-mediated pathways. Though mangrove growth and reproduction may be enhanced by nutrient enrichment, these increases may come at the expense of root allocation, microbial biodiversity, and C storage processes. Studies that claim nutrient enrichment is solely beneficial to mangroves fail to grasp the complexity of nutrient impacts on the biogeomorphic feedback that sustain these coastal wetlands and their resilience to extreme events within mangrove ecosystems (Clough et al., 1983; Robertson and Phillips, 1995; Erftemeijer et al., 2021). If we expect mangroves to continue to provide essential ecological services such as nutrient buffering, C sequestration, and coastal protection, we must aim for better agricultural practices and urban waste treatment to prevent the degradation of vital mangrove ecosystems and the essential functions they provide.

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No data was used for the research described in the article.

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