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7 8 9	Blue Nitrogen: Global Rates and Economic Importance
10	Ziyan Wang ^{1*} , Benoit Thibodeau ^{1,2*}
11	¹ The School of Life Sciences, The Chinese University of Hong Kong, New Territories, Shatin,
12	Hong Kong SAR, China
13	² Department of Earth and Environmental Sciences, The Chinese University of Hong Kong, New
14 15	Territories, Shatin, Hong Kong SAR, China
16 17 18 19	Corresponding authors: Ziyan Wang (1155186101@link.cuhk.edu.hk); Benoit Thibodeau (benoit.thibodeau@cuhk.edu.hk)
20	Key Points:
21 22	 Global mangroves currently remove 870 Gg N annually, with the highest rates occurring in deltaic mangrove systems.
23	 Removal of nitrogen by mangroves is highly vulnerable to global environmental changes.
24 25	 "Blue Nitrogen" credits offer a transformative opportunity to advance mangrove conservation and improve coastal water quality.

Abstract

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Nitrogen pollution drives widespread coastal ecosystem collapse. In this paper, we argue that 27 mangrove forests represent an undervalued natural mitigation solution for nitrogen pollution. 28 29 By performing a comprehensive meta-analysis, we reveal that mangroves remove 870 Gg N annually, which represents an economic value reaching \$8.7 billion via nitrogen credit-based 30 valuation. This value is more than 12 times higher than the annual carbon credits value derived 31 from mangrove carbon sequestration. Despite the substantial economic importance of 32 33 mangroves' nitrogen removal capacity, it remains largely overlooked in current conservation frameworks. Moreover, we argue that nitrogen removal by mangrove has a potential value that 34 could reach \$58 billion (over 5 million tonnes of nitrogen) under optimal conditions. We also 35 highlight critical environmental thresholds demonstrating that this service is vulnerable: 36 extreme eutrophication, rising mean annual temperature above 22°C, and hypersalinity all 37 suppress mangrove nitrogen removal capacity. Our findings provide the scientific foundation to 38 integrate "Blue Nitrogen" credits in larger nitrogen-credit framework, offering a transformative 39 40 financing mechanism for coastal water quality management that could reshape both mangrove conservation and nitrogen pollution mitigation strategies, worldwide. 41

Plain Language Summary

While coastal ecosystems are stressed by excessive nitrogen loads, key habitats within them, such as mangroves, provide a powerful nature-based solution. Our study establishes the first global benchmarks for mangrove nitrogen removal, revealing that mangroves remove 870 Gg N annually, representing an economic value of \$8.7 billion per year based on nitrogen credit valuation. This value could potentially reach \$58 billion under optimal conditions, highlighting the immense untapped potential of mangroves in nitrogen mitigation. These findings provide a compelling case for the establishment of a new "Blue Nitrogen" conservation market, which could revolutionize both mangrove conservation and nitrogen pollution mitigation strategies worldwide by offering a transformative financing mechanism for coastal water quality management.

1 Introduction 53 54 Nitrogen (N) release from human activities has increased by up to 50-fold since the early 1900s (Battye et al., 2017; Galloway et al., 2004). Still, creation of reactive N in China may double 55 between 2010 and 2050 under a business-as-usual scenario (Gu et al., 2015). This new N 56 impacts the Earth system, and it triggers a cascade of well-documented ecological crises in 57 coastal ecosystems, including eutrophication, harmful algal blooms, hypoxic "dead zones", and 58 59 substantial economic losses in fisheries and aquaculture (Breitburg et al., 2009; Galloway et al., 60 2004; Jessen et al., 2015). The severe economic damage of eutrophication is globally recognized, with annual losses in the billions of dollars consistently reported across diverse 61 watersheds in regions such as Europe (HELCOM, 2009), the United States of America (Dodds et 62 al., 2009), and China (Gu et al., 2015; Strokal et al., 2020). Furthermore, elevated nitrate levels 63 in water sources pose risks to human health (World Health Organization, 2022). Consequently, 64 these widespread impacts on both ecosystem integrity and public health have prompted 65 nations worldwide to implement costly coastal nutrient reduction programs (Boesch, 2002; 66 67 Greening & Elfring, 2002) or investigate the potential of other mitigation alternatives (Chen et al., 2025; Gu et al., 2023). Conventional engineered solutions to N pollution, such as 68 wastewater treatment, impose a substantial financial burden. Examples from the United States 69 70 of America show a growing \$81 billion annual funding gap for water infrastructure (American Society of Civil Engineers, 2021), alongside a doubling of residential wastewater bills in the past 71 72 decade (American Society of Civil Engineers, 2025). This funding gap highlights the urgent need for innovative and cost-effective alternatives to avoid further environmental damages. 73 Amidst this global challenge, mangrove forests offer a powerful nature-based solution. Their 74 unique, mostly anaerobic, carbon-rich sediment fosters microbial processes permanently 75 76 removing reactive N from the ecosystem (Adame & Lovelock, 2011; Fernandes et al., 2016). The primary process responsible for N removal is denitrification, the anaerobic reduction of nitrate 77 to N2O and N2. This process is thought to be fueled by the amount of available nitrate and 78 79 organic carbon (C) (Kraft et al., 2014; Rivera-Monroy & Twilley, 1996). A secondary pathway, anaerobic ammonium oxidation (anammox), can also contribute to N removal by converting 80

ammonium and nitrite directly into N₂, partly decoupled from the availability of C (Fernandes et

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al., 2012; Meyer et al., 2005). However, despite the increasing recognition of mangroves for 82 their capacity to buffer coastal waters from N pollution (Adame et al., 2019; Lee et al., 2009; 83 Wu et al., 2008), a robust global assessment is lacking. 84 85 Barriers to such an assessment are partly methodological and stem from the conflation of two 86 distinct measurement approaches —actual and potential rate assays. Actual rate 87 measurements (e.g., intact sediment cores, benthic chambers), capture realized N transformation rates under real-world constraints, including redox gradients, substrate 88 89 limitation, and diffusional barriers (Alongi et al., 2000; Trimmer et al., 2006; Whigham et al., 2009). Conversely, potential rate assays use homogenized slurries under optimal conditions 90 (e.g., strict anoxia, abundant substrate, and thorough mixing), thereby revealing the maximum 91 functional capacity of microbial communities (Amano et al., 2011; Dalsgaard et al., 2005). 92 93 However, the distinction between these two methods made it difficult to identify the specific 94 factors that govern net N-removal rate versus potential rates (Alongi, 2020; Reis et al., 2017). 95 An additional barrier is the lack of region-specific rate estimation. While biogeomorphic settings 96 of mangroves have successfully been used to refine global estimates of services like C 97 sequestration (Breithaupt & Steinmuller, 2022), a similar systematic analysis for mangrove N 98 removal has yet to be realized. It remains largely unknown how N removal varies across distinct 99 coastal settings, primarily deltaic, estuarine, open-coast and lagoonal (Worthington et al., 100 2020). This lack of a spatially explicit framework hinders rigorous upscaling estimates of the 101 global N-removal service. 102 Accurately quantifying global N removal is a critical step toward unlocking new conservation 103 opportunities for mangroves. As demonstrated by "Blue Carbon" science, valuing ecosystem services can powerfully drive conservation efforts (Costanza et al., 1997; Griscom et al., 2017; 104 105 Mcleod et al., 2011; Zhang et al., 2025). Likewise, when properly quantified, N removal by 106 coastal wetlands represents a valuable ecosystem service that should be incorporated into conservation decision-making and policy frameworks (Daily et al., 2009). This approach can help 107 coastal regions advance toward the goal of N neutrality — a state of zero net reactive N release 108 109 to the environment (Chen et al., 2025; Leip et al., 2014).

Our objective is therefore to provide a clear assessment of mangrove N removal through a global compilation and meta-analysis of actual and potential rates, and to identify their respective drivers. Moreover, we provide a basic framework for the economic valuation of N removal by mangroves based on the established economic benchmarks for N reduction.

2 Methods

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2.1 Meta-analysis

We conducted a bibliographic search based on the Web of Science database using the search terms "mangrove" AND ("denitrification" OR "anammox" OR "nitrate reduction" OR "nitrogen removal" OR "nitrogen loss"), for articles published up to April 2025. This search yielded 924 papers, which were manually screened to retain only those studies reporting empirical N removal rates from fresh mangrove sediment and ambient conditions. Reference lists were also checked for additional studies. The final dataset for our meta-analysis comprised 51 published studies (screening procedure referring to Figure S1) and was augmented with an unpublished dataset from our own ongoing research (available in Supplementary Data). We created a dataset distinguishing between two fundamental metrics: (1) actual rates, measured in intact sediment cores using ¹⁵N labeling, N₂:Ar ratio, or acetylene inhibition techniques; and (2) potential rates, measured by in homogenized sediment slurries using ¹⁵N labeling or acetylene inhibition techniques. Our data compilation revealed that studies using the N_2 gas flux technique report systematically higher and more variable actual rates than other methods (Figure S2). In line with previous work identifying this as a methodological artifact (Robert Hamersley & Howes, 2005), these studies were therefore excluded to avoid overestimating true N removal. Throughout this study, total N removal is defined as the sum of denitrification and anammox rates. This meta-analysis therefore establishes a lower bound for total mangrove N removal, as it incorporates historical methods (e.g., early ¹⁵N labeling, acetylene inhibition techniques) that did not detect anammox inherently and thus reflect denitrification alone. We explicitly address and quantify the potential magnitude of this

underestimation in our Results and Discussion (Section 3.1).

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We standardized actual rates to areal units (µmol N m⁻² h⁻¹) and potential rates to volumetric units (mmol N m⁻³ h⁻¹), using either the reported sediment density or a representative value of 1.88 g cm⁻³ to convert mass-based rates when necessary (Hou et al., 2015). Furthermore, to enable a direct comparison, we calculated a conservative areal flux from potential rates by normalizing them over a 1-cm active sediment depth. We extracted a suite of key environmental variables and classified sites by coastal environmental setting, ambient trophic status, and sediment type. We sourced the parameters from the text, tables, and supplementary materials of each publication, with graphical data extracted using WebPlotDigitizer. A complete description of all variables is provided in Text S1 and Table S1. To upscale our N-removal rates globally, we used setting-specific mean rates to the published area estimates for four coastal environmental settings: deltaic (54,972 km²), estuarine (37,411 km²), open coast (28,493 km²), and lagoonal (14,993 km²), summing to a total mangrove area of 135,869 km² (Worthington et al., 2020). We acknowledge that our calculations may not capture the full range of N-removal variability, as our approach averages seasonal and vertical scales. Nevertheless, it provides a robust first estimate of the mean annual N-removal service provided by the world's mangroves. 2.2 Statistical analysis All statistical analyses and data visualizations were performed in R (v. 4.3.0). As the raw data did not meet normality assumptions (Shapiro-Wilk test, p<0.05), a \log_{10} transformation was applied. The transformed means and 95% confidence intervals were calculated and are presented as back-transformed values (referred to as "adjusted means") (Breithaupt & Steinmuller, 2022). For comparison, medians and arithmetic means from the untransformed data were also reported. To compare N-removal rates between groups, we used appropriate parametric (one-way ANOVA with Tukey's post-hoc tests) or non-parametric (Kruskal-Wallis with Dunn's post-hoc tests) tests.

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Linear mixed effects models were used to evaluate relationships between N removal and environmental parameters. To further identify the key environmental drivers of potential N removal and capture non-linear relationships, we developed a random forest model using the R package randomForest (Liaw & Wiener, 2002). The model's predictive performance was validated using 10-fold cross-validation. We assessed predictor importance based on the percent increase in mean squared error (%IncMSE) and visualized the marginal effects of the most influential variables using partial dependence plots (PDPs) via the pdp package. Full details of the model parameters are provided in Text S2. 2.3 Ecosystem service valuation We estimated the economic value of mangrove N removal using a market-based credit approach. We adopted a value of \$ 10,053 per ton of N (in 2022 USD), derived from the successful Connecticut Nitrogen Credit program (Dykes, 2022). This specific value was selected because it represents a conservative median from our review of representative valuation methods (Table S2) and is also grounded in a mature, policy-relevant market, ensuring its applicability. To provide a direct and methodologically consistent comparison for our annual N-removal valuation, we developed a tailored estimate for the annual service of mangrove carbon sequestration that aligns with the specific coastal geomorphic settings of our analysis – a refinement absent from most previous "blue carbon" valuation (Pendleton et al., 2012; Zeng et al., 2021; Zhang et al., 2025). Our valuation is based on biogeomorphology-specific C sequestration rates (Breithaupt & Steinmuller, 2022), a CO₂ equivalence conversion factor of 3.67 (Zhang et al., 2025), and an average voluntary carbon market price of \$ 6.30 per ton of CO2e from Forest Trends' Ecosystem Marketplace reports in 2020-2024

3 Results and Discussion

3.1 Global compilation of mangrove N removal

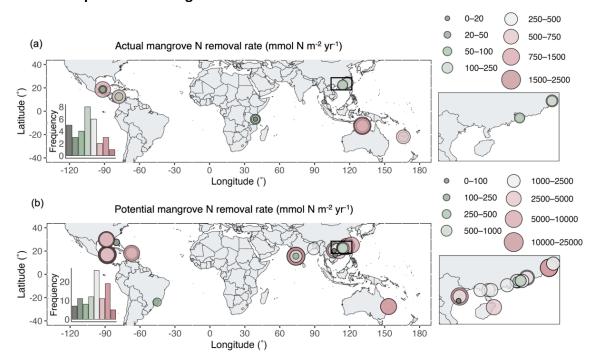
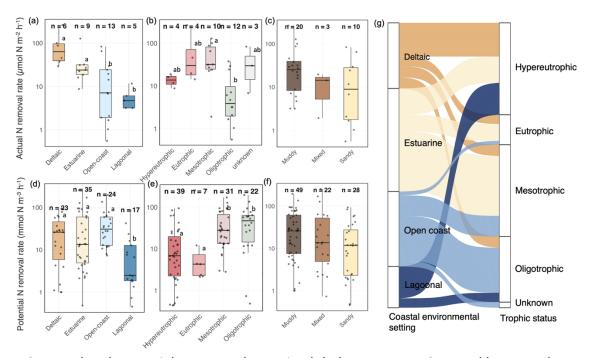


Figure 1. Global distribution and magnitude of mangrove N removal. Maps show (a) site-specific actual rates, (b) site-specific potential rates. Inset histograms illustrate the frequency distribution of the sites across calculated value categories.

Our global meta-analysis provides a new and robust baseline for mangrove N removal based on data from 33 actual and 99 potential rate studies (Figure 1). The adjusted mean of actual N-removal rates was 14.80 μ mol N m⁻² h⁻¹ (95% CI: 8.97–24.44), derived from log-transformed values to account for data skewness (Breithaupt & Steinmuller, 2022). This value is more conservative than the median of 27.67 μ mol N m⁻² h⁻¹ and the arithmetic mean of 35.09 μ mol N m⁻² h⁻¹, which were influenced by a few extremely high measurements. As expected, potential N-removal rates are higher, with an adjusted mean of 140.78 μ mol N m⁻² h⁻¹ (95% CI: 103.96–190.65) that is similar to the median (156.04 μ mol N m⁻² h⁻¹) but much lower than the arithmetic mean (340.59 μ mol N m⁻² h⁻¹).

Our findings support the idea that mangroves are N-removal hotspots at the land-sea interface,
as their representative actual N-removal rate (14.8 μ mol N m ⁻² h ⁻¹) is nearly double the global
average for terrestrial soils (~7.5 μ mol N m ⁻² h ⁻¹ ; Seitzinger et al., 2006) and higher than the
mean rate observed in marine sediments (~8.7 μ mol N m $^{-2}$ h $^{-1}$; Chang et al., 2024). Based on
paired measurements of denitrification and anammox, our compilation also revealed that
denitrification is the dominant N-removal pathway in global mangrove sediments, while
anammox accounts on average for 23.2% of actual and 11.7% of potential N removal. Applying
these proportions as a preliminary correction factor to historical studies that only measured
denitrification rates, we found that the total N removal may have been systematically
underestimated by 8% (actual) or 6% (potential). While this correction carries uncertainty, it
indicates a consistent downward bias in assessments of mangrove N-removal services.
Globally, we estimated that mangroves provide an annual N removal of 867 Gg N yr ⁻¹ (95% Cl:
234-1503), based on an area-weighted upscaling that accounts for coastal environmental
settings. Notably, these actual rates represent only about 15% of the ecosystem's full latent
capacity. We estimate that the mangrove N-removal potential is $^{\sim}$ 5670 Gg N yr $^{\text{-1}}$, a theoretical
capacity that could offset 1.8-3.1% of total anthropogenic reactive N created annually
(Galloway et al., 2021), highlighting their biogeochemical importance while occupying less than
0.1% of the Earth's land surface.

3.2 Decoupled controls on N removal



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Figure 2. Actual and potential N-removal rates in global mangroves. Grouped by coastal environmental settings (a, d); surrounding water trophic status (b, e); sediment types within mangrove forests (c, f). Boxplots display the median (line), interquartile range (box), and individual data points. Different letters denote statistically significant differences among groups (Kruskal-Wallis with Dunn's post-hoc tests, p<0.05). (h) Distribution of coastal environmental settings across trophic status categories.

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By comparing the different types of mangroves, we observed that actual N-removal rates were highest in deltaic and estuarine systems and in eutrophic waters (Figure 2a,b), reflecting that greater nutrient concentration generally supports higher N-removal activity (Rivera-Monroy & Twilley, 1996; Statham, 2012). This linkage was illustrated by the very strong positive correlation observed between actual N-removal rates and overlying water nitrate concentrations across our dataset (R= 0.94, p<0.001; Figure S3b). However, mangroves in opencoast and oligotrophic settings demonstrated a removal potential that was comparable to or even superior to their nutrient-rich counterparts (Figure 2d & e, Table S3). We also found a moderate but significant negative correlation between potential N-removal capacity and ambient overlying nitrate levels throughout the dataset (R = -0.42, p < 0.05; Fig. S3e).

Therefore, while actual rates are strongly governed by overlying water nitrate concentration, potential rates appear to be determined by other factors, as nitrate is not limiting in these experiments.

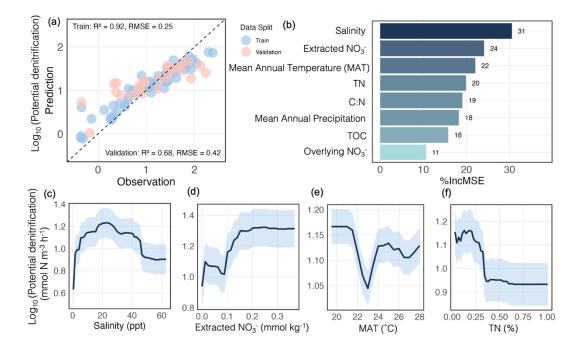


Figure 3. Predictive modeling of potential denitrification rates using a random forest model. (a) Performance metrics of the model, showing the relationship between the training and validation sets. (b) The importance (increase in mean squared error, %IncMSE) of predictors of potential denitrification rates. (c)-(f) partial dependence plots showing the marginal effect of the four most influential variables on the potential denitrification prediction. The solid line represents the mean model prediction, and the shaded area indicates the standard deviation.

To understand the mechanisms of N-removal potential, we focused on potential denitrification, which serves as a robust proxy for total N removal. This is supported by its dominance as the primary N-removal pathway and its strong correlation with anammox (R = 0.7, p<0.001, Fig. S4b), a coupling consistent with broader patterns in aquatic ecosystems (Xu et al., 2025).

Accordingly, we developed a random forest model to predict our potential denitrification rates from a suite of abiotic factors. The model demonstrated strong predictive power, with a ten-

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fold cross-validation capturing 64% of the variation in global rates (cross-validated R²=0.64). Therefore, the model provides a reliable tool for predicting rates and identifying their key environmental controls. The resulting variable importance analysis revealed that local biogeochemical factors, especially salinity and sediment-extracted nitrate concentration, are the most important drivers (Figure 3b). The importance of salinity as a key determinant suggests a direct link to the high N-removal potential observed in open-coast mangroves. We tested this link directly by examining the relationship between salinity and potential N removal within each coastal environmental setting (Figure S5) and confirmed a significant positive correlation in open-coast mangroves (R=0.52, p<0.01). This strong salinity dependence can be interpreted through two possible mechanisms. First, high salinity acts as a powerful ecological filter, potentially selecting for a more specialized and efficient denitrifying microbial community (Torregrosa-Crespo et al., 2023). Additionally, these high-salinity, organic-rich environments can provide a source of sulfide with the constant supply of sulfate from seawater, offering a potent alternative electron donor for denitrification and increasing the system's overall N removal (Cojean et al., 2020; Plummer et al., 2015; Wang et al., 2024). The high potential in oligotrophic systems could also be a great example of the "feast and famine" ecological concept (Koch, 2001; Poindexter, 1981). Though never invited to a feast, nutrient-starved communities even evolve a high capacity for nutrient uptake, as a fitness strategy to catch any resource pulse (Zhu & Dai, 2024). Concurrently, our model identified sediment nitrate as a key predictor of potential rates, likely reflecting the baseline capacity of the resident denitrifying community. The potential rate assay stimulates a "feast" by supplying abundant nitrate. The resulting explosive response is therefore driven by both the high affinity and inherent capacity of these famine-adapted communities. In contrast, communities in eutrophic systems that have already adapted to a constant feast show a less dramatic response.

3.3 Implications for coastal resilience

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beyond a critical stress point.

Our analysis reveals that N-removal response to environmental drivers is often non-linear, with critical thresholds that have profound implications for mangrove functioning under future global change scenarios. For instance, our observational data show rates of both actual and potential N removal peak in mesotrophic waters before declining in hypereutrophic waters (Figure 2b & 2e), suggesting suppression by extreme nutrient loading. This finding warns that as coastal eutrophication worsens, this vital purification service by mangroves could fail precisely where it is most needed. Similarly, a climatic threshold is evident from actual rates being significantly lower in regions with higher mean annual temperatures (MAT) (Figure S6b). Our random forest model independently identified that potential denitrification could decline beyond an optimal temperature of around 22°C (Figure 3e). Contrary to assumptions based on the relationship between temperature and metabolic rates, our model suggests that the long-term increases in MAT projected by the IPCC (2023) may systematically suppress, and not enhance, the Nremoval capacity of mangroves, likely due to indirect effects like reduced soil moisture and decreased in anaerobic areas (Chen et al., 2023). This is similar to what has been shown in seagrasses (Bass et al., 2025). Further, while the effect of salinity on N removal is broadly positive, the effect at high concentrations (Figure 3d, >40 ppt) suggests that hypersaline conditions may impose osmotic stress that constrains the actual and potential microbial activity (Li et al., 2024), common in lagoons (Figure 2a & 2d, Figure S7c) with restricted exchange (Mudge et al., 2008). This implies that sea-level rise and saltwater intrusion will have complex and diverging effects, potentially boosting N removal in historically fresher coastal systems while pushing already saline lagoons

3.4 Economic analysis and outlook for N neutrality

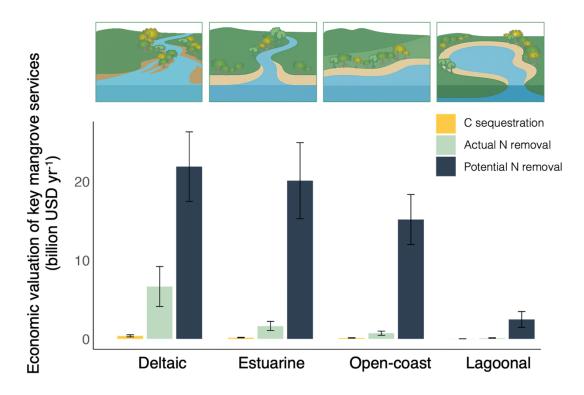


Figure 4. Economic credit valuation of annual N removal and C sequestration services in deltaic, estuarine, open-coast, and lagoonal mangroves. Bars represent the arithmetic mean of each valuation and error bars represent the 95% confidence interval.

Quantifying the economic value of N removal via denitrification and anammox in mangroves reveals a significant and previously unrecognized benefit of these ecosystems. We performed a market-based valuation using a N credit price of \$10,053 per ton N in 2022 USD (Dykes, 2022) and estimated the value of the actual service at \$8.7 billion annually (95% CI: 2.4-15.1). This global value is highly concentrated in deltaic mangroves (\$7.92 billion yr⁻¹) due to their large area and the highest N-removal rates. Moreover, the value of the total potential N-removal capacity reaches around \$57 billion annually, highlighting the importance of improving our understanding of the drivers of N-removal in these ecosystems. This is significant as the societal cost of N pollution by agriculture has been estimated from €35 to €230 billion per year in Europe (Gu et al., 2021).

In systems like deltaic and estuarine mangroves, where N removal and C sequestration are both highly efficient (Figure 4), the annual economic value of N removal can be an order of magnitude greater than that of carbon sequestration. Furthermore, our analysis reveals that open-coast systems, which may be undervalued in a purely carbon-focused framework due to lower C accumulation (Breithaupt & Steinmuller, 2022), harbour a much higher value of N removal. Therefore, integrating the value of N-removal into the conservation framework may contribute to the preservation of these key ecosystems, as integrated C and N managements have been suggested as a potentially effective solution for China (Xu et al., 2025).

Our valuation provides a clear economic case for integrating N cycling into ecosystem service frameworks. The merit of a robust mangrove "Blue Nitrogen" market becomes evident, offering a cost-efficient pathway for coastal zones to meet water quality goals compared to engineered solutions alone. By properly valuing this service, we can unlock new streams of conservation finance and create powerful incentives for strategic restoration and smarter investments into N neutrality and sustainable coastal development.

5 Conclusions

This global meta-analysis establishes the first comprehensive benchmarks of N removal in mangrove sediments, quantifying actual removal at 870 Gg N yr⁻¹ and revealing a latent potential up to 5,670 Gg N yr⁻¹. Our study uncovers a decoupling between the drivers of actual and potential N removal. Specifically, actual N-removal rates are primarily driven by nutrient loading, whereas the potential capacity is shaped by seawater chemistry and microbial strategies. We also identified critical environmental thresholds for nutrients, temperature, and salinity, clearly demonstrating that mangrove N-removal services are vulnerable to ongoing global change. Using an N-credit valuation approach, we estimate the currently unrecognized economic value of this "Blue Nitrogen" service at \$8.7 billion yr⁻¹, more than 12 times the annual carbon credits value of mangrove carbon sequestration. Together, these findings lay the groundwork for a "Blue Nitrogen" framework, creating a new avenue for conservation finance and policy aimed at safeguarding water quality and the resilience of our coastlines.

345	Supplementary Information
346	Additional supporting materials are available in the Supplementary Information of this article.
347	Data Availability Statement
348	All data used in this meta-analysis are available in the Figshare repository
349	(https://doi.org/10.6084/m9.figshare.30454196).
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356	Conflict of Interest Disclosure
357	The authors declare there are no conflicts of interest for this manuscript.
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