A New Optic on Mangrove Conservation: Blue Nitrogen

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Abstract

Nitrogen (N) pollution is a primary driver of widespread coastal ecosystem collapse, and mangrove forests represent an undervalued natural mitigation solution for nitrogen removal. Through a comprehensive meta-analysis, we reveal that globally, mangroves remove 870 Gg N annually, which represents only 15% of their theoretical maximum capacity of 5,670 Gg N yr^{-1}. The economic value of this service reaches 8.7 billion annually via N credit-based valuation, more than 12 times the annual carbon credits value of mangrove carbon sequestration, yet this remains entirely unrecognized in current conservation frameworks. We also highlight critical environmental thresholds demonstrating that this service is vulnerable: extreme eutrophication, rising mean annual temperature above 22°C, and hypersalinity all suppress mangrove nitrogen removal capacity. Our findings provide the scientific foundation for "Blue Nitrogen" credits, offering a transformative financing mechanism for coastal water quality management that could reshape both mangrove conservation and nitrogen pollution mitigation strategies, worldwide.

Synopsis statement

Mangroves remove nitrogen pollution globally, offering untapped economic value and a transformative opportunity for conservation and coastal water quality management.

1. Introduction

Nitrogen (N) release from human activities has increased by up to 50-fold since the early 1900s and is reaching new heights every year [1,2]. This new N impacts the Earth system, and it triggers a cascade of well-documented ecological crises in coastal ecosystems, including eutrophication, harmful algal blooms, hypoxic "dead zones", and substantial economic losses in fisheries and aquaculture [2–4]. The severe economic damage of eutrophication is globally recognized, with annual losses in the billions of dollars consistently reported across diverse watersheds in regions such as Europe [5], the United States of America [6], and China [7]. Furthermore, elevated nitrate levels in water sources pose risks to human health [8]. Consequently, these widespread impacts on both ecosystem integrity and public health have prompted nations worldwide to implement costly coastal nutrient reduction programs [9,10]. Conventional engineered solutions to N pollution, such as wastewater treatment, impose a substantial financial burden. Examples from the United States of America show a growing $81 billion annual funding gap for water infrastructure [11], alongside a doubling of residential wastewater bills in the past decade [12]. This financial unsustainability highlights the urgent need for innovative and cost-effective alternatives.

Amidst this global challenge, mangrove forests offer a powerful nature-based solution. Their unique, mostly anaerobic, carbon-rich sediment fosters microbial processes permanently removing reactive N from the ecosystem [13,14]. The primary process responsible for N removal is denitrification, the anaerobic reduction of nitrate to N_2O and N_2. This process is thought to be fueled by the amount of available nitrate and organic carbon (C) [15,16]. A secondary pathway, anaerobic ammonium oxidation (anammox), can

61 also contribute to N-removal by converting ammonium and nitrite directly into N_2, partly
62 decoupled from the availability of C [17,18]. However, despite the increasing recognition of
63 mangroves for their capacity to buffer coastal waters from N pollution [19–21], a robust
64 global assessment is lacking.

65 Barriers to such an assessment are partly methodological and stem from the conflation of
66 two distinct measurement approaches —actual and potential rate assays. Actual rate
67 measurements (e.g., intact sediment cores, benthic chambers), capture realized N
68 transformation rates under real-world constraints, including redox gradients, substrate
69 limitation, and diffusional barriers [22–24]. Conversely, potential rate assays use
70 homogenized slurries under optimal conditions (e.g., strict anoxia, abundant substrate,
71 and thorough mixing), thereby revealing the maximum functional capacity of microbial
72 communities [25,26]. However, the distinction between and reconciliation across these two
73 methods has not been consistently and compellingly achieved in previous syntheses,
74 making it difficult to identify the specific factors that govern N-removal in actual or
75 potential states [27,28].

76 An additional barrier is the lack of region-specific rate estimation. While biogeomorphic
77 settings of mangroves have successfully been used to refine global estimates of services
78 like C sequestration [29], a similar systematic analysis for mangrove N removal has yet to
79 be realized. It remains largely unknown how N removal varies across distinct coastal
80 settings, primarily deltaic, estuarine, open-coast and lagoonal [30]. This lack of a spatially
81 explicit framework hinders rigorous upscaling estimates of the global N-removal service.

Accurately quantifying global N removal is a critical step toward unlocking new conservation opportunities for mangroves. As demonstrated by "Blue Carbon" science, valuing ecosystem services can powerfully drive conservation efforts [31–34]. Likewise, when properly quantified, N removal by coastal wetlands represents a valuable ecosystem service that should be incorporated into conservation decision-making and policy frameworks [35]. This approach can help coastal regions advance toward the goal of N neutrality — a state of zero net reactive N release to the environment [36].

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 framework for the economic valuation of N removal by mangroves based on the established economic benchmarks for N reduction.

2. Methods

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 ^{15}N labeling, N_2:Ar ratio, or acetylene inhibition techniques; and (2) potential rates, measured by in homogenized sediment slurries using ^{15}N 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 [37], 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 ^{15}N 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).

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 [38]. 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.

127 To upscale our N-removal rates globally, we used setting-specific mean rates to the
128 published area estimates for four coastal environmental settings: deltaic (54,972 km^2),
129 estuarine (37,411 km^2), open coast (28,493 km^2), and lagoonal (14,993 km^2), summing to
130 a total mangrove area of 135,869 km^2 [30]. We acknowledge that our calculations may not
131 capture the full range of N-removal variability as our approach averages seasonal and
132 vertical scales. Nevertheless, it provides a robust estimate of the mean annual N-removal
133 service provided by the world's mangroves.

134 **2.2 Statistical analysis**

135 All statistical analyses and data visualizations were performed in R (v. 4.3.0). As the raw
136 data did not meet normality assumptions (Shapiro-Wilk test, $p<0.05$), a $\log_{10}$
137 transformation was applied and the transformed means and 95% confidence intervals
138 were calculated and are presented as back-transformed values (referred to as "adjusted
139 means") [29]. For comparison, medians and arithmetic means from the untransformed data
140 were also reported. To compare N-removal rates between groups, we used appropriate
141 parametric (one-way ANOVA with Tukey's post-hoc tests) or non-parametric (Kruskal-
142 Wallis with Dunn's post-hoc tests) tests.

143 Linear mixed effects models were used to evaluate relationships between N removal and
144 environmental parameters. To further identify the key environmental drivers of potential
145 N removal and capture non-linear relationships, we developed a random forest model
146 using the R package randomForest [39]. The model's predictive performance was validated
147 using 10-fold cross-validation. We assessed predictor importance based on the percent
148 increase in mean squared error (%IncMSE) and visualized the marginal effects of the

149 most influential variables using partial dependence plots (PDPs) via the pdp package.
150 Full details of the model parameters are provided in Text S2.

151 **2.3 Ecosystem service valuation**

152 We estimated the economic value of mangrove N removal using a market-based credit
153 approach. We adopted a value of $ 10,053 per ton of N (in 2022 USD), derived from the
154 successful Connecticut Nitrogen Credit program [40]. This specific value was selected
155 because it represents a conservative median from our review of representative valuation
156 methods (Table S2) and is also grounded in a mature, policy-relevant market, ensuring its
157 real-world applicability.

158 To provide a direct and methodologically consistent comparison for our annual N-
159 removal valuation, we developed a tailored estimate for the annual service of mangrove
160 carbon sequestration that aligns with the specific coastal geomorphic settings of our
161 analysis – a refinement absent from most previous "blue carbon" valuation [33,41,42]. Our
162 valuation is based on biogeomorphology-specific C sequestration rates[29], a CO_2
163 equivalence conversion factor of 3.67 [33], and an average voluntary carbon market price of
164 $ 6.30 per ton of CO_2e from Forest Trends' Ecosystem Marketplace reports in 2020-2024
165 (https://ecosystemmarketplace.com).

3. Result and Discussion

3.1 Global compilation of mangrove N removal

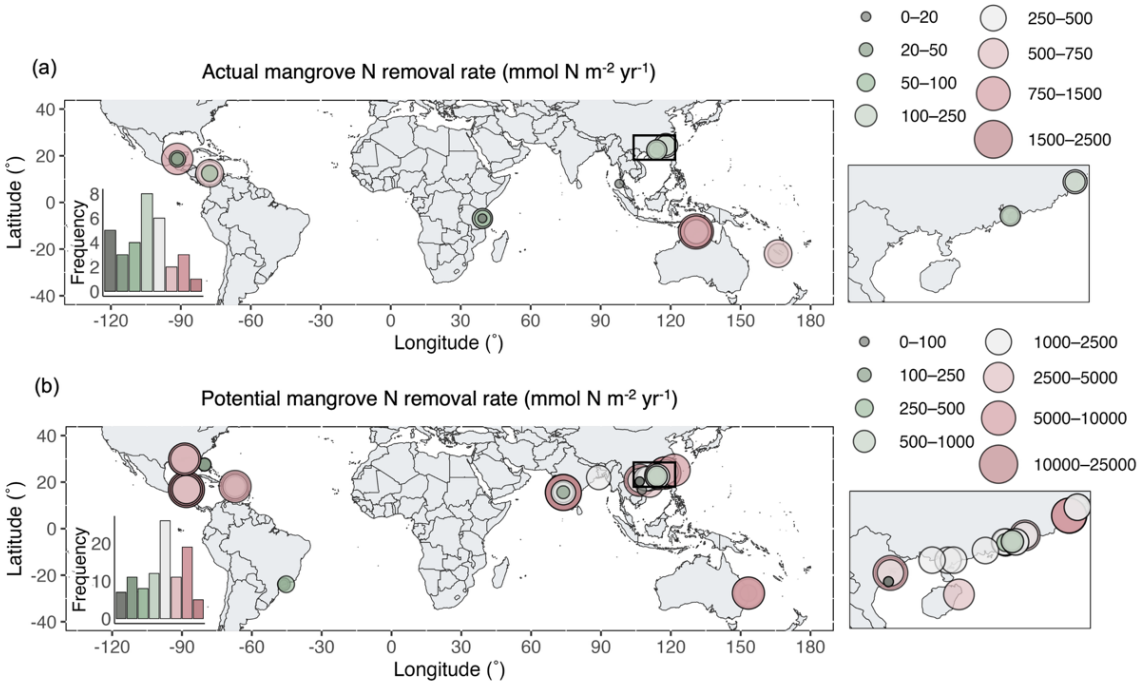


Figure 1. Global distribution and magnitude of mangrove N removal. Maps show (a) site-specific actual rates, (b) site-specific potential rates. Inset histograms illustrate the frequency distribution of the sites across calculated value categories.

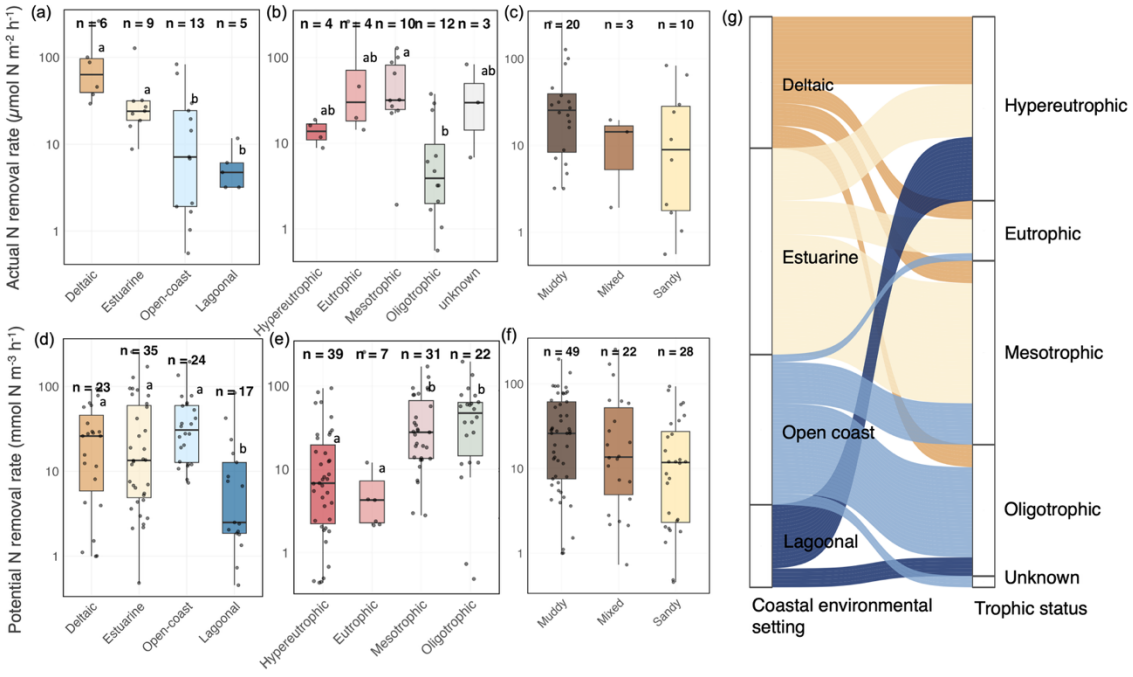
Our global meta-analysis provides a new and robust baseline for mangrove N removal based on data from 33 actual and 99 potential rate studies (Figure 1). The adjusted mean of actual N-removal rates was 14.80 μmol N m^{-2} h^{-1} (95% CI: 8.97–24.44), derived from log-transformed values to account for data skewness [29]. This value is more conservative than the median of 27.67 μmol N m^{-2} h^{-1} and the arithmetic mean of 35.09 μmol 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 μmol N m^{-2} h^{-1} (95% CI:

103.96–190.65) that is similar to the median (156.04 μmol N m^{-2} h^{-1}) but much lower than the arithmetic mean (340.59 μmol 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 μmol N m^{-2} h^{-1}) is nearly double the global average for terrestrial soils (~7.5 μmol N m^{-2} h^{-1}) [43] and higher than the mean rate observed in marine sediments (~8.7 μmol N m^{-2} h^{-1}) [44]. 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 ~ 5670 Gg N yr^{-1}, a theoretical capacity that could offset 1.8-3.1% of total anthropogenic reactive N created annually [45], highlighting their biogeochemical importance while occupying less than 0.1% of the Earth's land surface.

200 ### 3.2 Decoupled controls on N removal



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

208 By comparing the different types of mangroves, we observed that actual N-removal rates
209 were highest in deltaic and estuarine systems and in eutrophic waters (Figure 2a,b),
210 reflecting that greater nutrient concentration generally supports higher N-removal activity
211 [16,46]. This linkage was illustrated by the very strong positive correlation observed between
212 actual N-removal rates and overlying water nitrate concentrations across our dataset ($R=$
213 0.94, $p<0.001$; Figure S3b). However, mangroves in open-coast and oligotrophic settings

demonstrated a removal potential that was comparable to or even superior to their nutrient-rich counterparts (Figure 2d & e, Table S3). Even more surprisingly, we 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 limited.

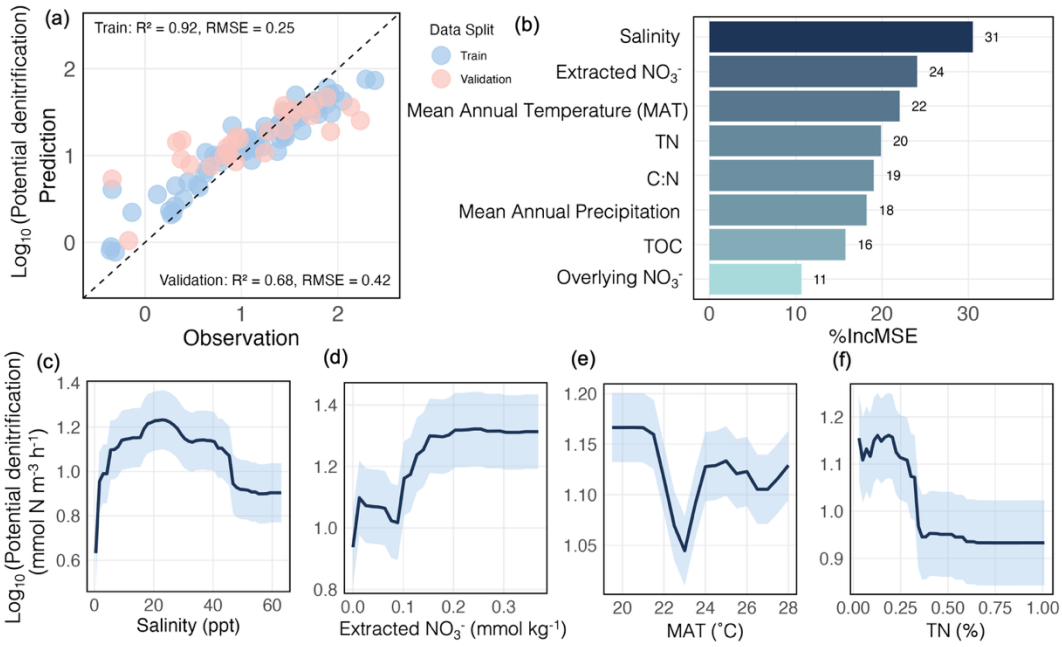


Figure 3. Predictive modeling of potential denitrification rates using a random forest model. (a) Performance metrics of the model, showing the relationship between the training and validation sets. (b) the importance (increase in mean squared error, %IncMSE) of predictors of potential denitrification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

227 denitrification prediction. The solid line represents the mean model prediction, and the
228 shaded area indicates the standard deviation.

229 To understand the mechanisms of N-removal potential, we focused on potential
230 denitrification, which serves as a robust proxy for total N removal. This is supported by
231 its dominance as the primary N-removal pathway and its strong correlation with
232 anammox ($R = 0.7$, $p<0.001$, Fig. S4b), a coupling consistent with broader patterns in
233 aquatic ecosystems [47].

234 Accordingly, we developed a random forest model to predict our potential denitrification
235 rates from a suite of abiotic factors. The model demonstrated strong predictive power,
236 with a ten-fold cross-validation capturing 64% of the variation in global rates (cross-
237 validated $R^2=0.64$). Therefore, the model provides a reliable tool for predicting rates and
238 identifying their key environmental controls. The resulting variable importance analysis
239 revealed that local biogeochemical factors, especially salinity and sediment-extracted
240 nitrate concentration, are the most influential predictors (Figure 3b).

241 The importance of salinity as a top-ranked predictor suggests a direct link to the high N-
242 removal potential observed in open-coast mangroves. We tested this link directly by
243 examining the relationship between salinity and potential N removal within each coastal
244 environmental setting (Figure S5) and confirmed a significant positive correlation in
245 open-coast mangroves ($R=0.52$, $p<0.01$). This strong salinity dependence can be
246 interpreted through two possible mechanisms. First, high salinity acts as a powerful
247 ecological filter, potentially selecting for a more specialized and efficient denitrifying
248 microbial community [48]. Additionally, these high-salinity, organic-rich environments can

249 provide a source of sulfide with the constant supply of sulfate from seawater, offering a
250 potent alternative electron donor for denitrification and increasing the system's overall N
251 removal [49–51].

252 The high potential in oligotrophic systems may be a great example of the "feast and
253 famine" ecological theory [52,53]. Though never invited to a feast, nutrient-starved
254 communities even evolve a high capacity for nutrient uptake, as a fitness strategy to catch
255 any resource pulse [54]. Concurrently, our model identified sediment nitrate as a key
256 predictor of potential rates, likely reflecting the baseline capacity of the resident
257 denitrifying community. The potential rate assay stimulates a "feast" by supplying
258 abundant nitrate. The resulting explosive response is therefore driven by both the high
259 affinity and inherent capacity of these famine-adapted communities. In contrast,
260 communities in eutrophic systems that have already adapted to a constant feast show a
261 less dramatic response.

262 **3.3 Implications for coastal resilience**

263 Our analysis reveals that N-removal responses to environmental drivers are often non-
264 linear, with critical thresholds that have profound implications for mangrove functioning
265 under future global change scenarios. For instance, our observational data show rates of
266 both actual and potential N removal peak in mesotrophic waters before declining in
267 hypereutrophic waters (Figure 2b & 2e), suggesting suppression by extreme nutrient
268 loading. This finding warns that as coastal eutrophication worsens, this vital purification
269 service by mangroves could fail precisely where it is most needed.

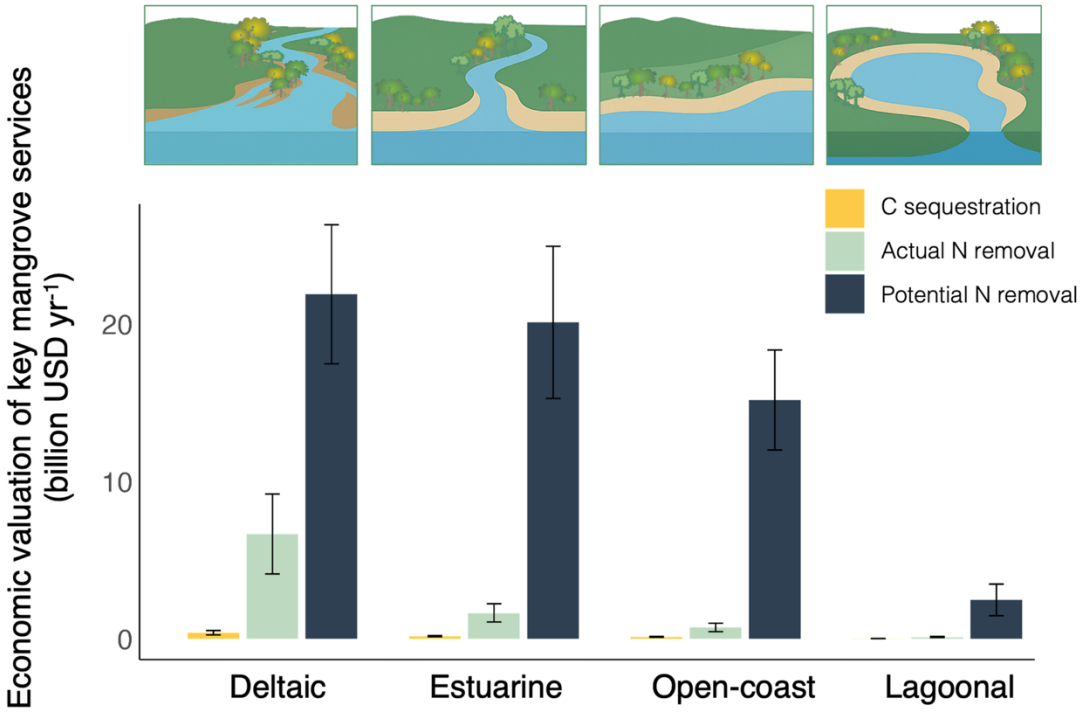
Similarly, a climatic threshold is evident from actual rates being significantly lower in regions with higher mean annual temperatures (MAT) (Figure S6b). Our random forest model independently identified that potential denitrification could decline beyond an optimal temperature of around 22˚C (Figure 3e). This serves as a critical caution for global warming. Contrary to simple metabolic assumptions, the long-term increases in MAT projected by the IPCC [55] may systematically suppress, not enhance, the N-removal capacity of mangroves, likely due to indirect effects like reduced soil moisture and less anaerobic conditions[51].

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 [56], common in lagoons (Figure 2a & 2d, Figure S7c) with restricted exchange [57]. 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 beyond a critical stress point.

3.4 Economic analysis and outlook for N neutrality

Translating the large-scale N-removal service into economic metrics reveals its previously unaccounted-for, important economic value. We performed a market-based valuation using a nitrogen credit price of $10,053 per ton N in 2022 USD [40] and estimated the value of the actual service at $8.7 billion annually (95% Cl: 2.4-15.1) through area-weighed upscaling. This global value is highly concentrated in economic hotspots: deltaic mangroves alone ($7.92 billion yr^{-1}) account for the majority of the total

292 actual value, owing to their large area with the highest actual N-removal rates. Beyond
293 the actual service, the value of total potential N-removal capacity reaches around $57
294 billion annually, highlighting the importance of producing new knowledge about drivers
295 of N-removal in these ecosystems.



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

300 In "dual-benefit" systems like deltaic and estuarine mangroves, where N removal and C
301 sequestration are both highly efficient (Figure 4), the annual economic value of N
302 removal can be an order of magnitude greater than that of carbon sequestration.
303 Furthermore, our analysis reveals that open-coast systems, which may be undervalued in

a purely carbon-focused framework due to lower C accumulation [29], harbour a much higher value of N removal.

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.

Supplementary Information

All supplementary materials are available at DOI: 10.6084/m9.figshare.30454196.

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