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ORIGINAL RESEARCH PAPER

The role of nutrient availability and resorption efficiency and their impact on nutrient conservation in mangroves

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ABSTRACT

BACKGROUND AND OBJECTIVES: Nutrient availability influences mangrove forest structure and productivity. The conversion of mangroves into aquaculture ponds can lead to significant disturbances, resulting in long-term consequences associated with the clearing of vegetation and changes in the physico-chemical properties of the soil. These alterations may subsequently restrict the availability of essential nutrients, including nitrogen and phosphorus. Consequently, nutrient limitations can constrain mangrove growth and development. Conventional indicators of nutrient limitation are founded on the analysis of leaf nutrient and nutrient resorption ratios, drawing from datasets collected in terrestrial and temperate forest environments. However, these indices may not be applicable to mangroves due to the prevalence of a wide range of environmental settings and occurrences of disturbances. In the Philippines, mangrove ecosystems are represented by diverse stand types, including natural or intact mangroves, restored or planted mangroves, and recolonized stands, which are naturally revegetated abandoned ponds. These different stand types are perceived to have different levels of nutrient availability and resorption capabilities. This study aims to investigate the changes in soil and leaf nutrient concentrations of nitrogen and phosphorus, leaf nitrogen to phosphorus ratio, nitrogen and phosphorus resorption efficiencies, and nitrogen resorption efficiency to phosphorus resorption efficiency ratio across a chronosequence of restored and recolonized stands (with intact natural stands as reference sites) in Ormoc Bay, Philippines.
METHODS: Soil and leaf samples were obtained from both seedlings and mature trees across each vegetation plot in restored, recolonized, and natural stands, totaling 30 plots. Soil (total nitrogen and available phosphorus) and leaf (total nitrogen and total phosphorus) samples were analyzed for nutrient concentrations. The calculations were performed to determine the leaf nitrogen to phosphorus ratio, nitrogen resorption efficiency, phosphorus resorption efficiency, and the ratio of nitrogen resorption efficiency to phosphorus resorption efficiency based on the nutrient concentrations.
FINDINGS: While there was a marked difference in the nutrient composition of soil and leaves across various stand types, the data did not indicate any clear age-related patterns in the restored and recolonized stands. Soil nutrients were not correlated with leaf nutrients suggesting that soil nutrient availability does not necessarily translate to nutrient absorption and accumulation in the leaves. Nitrogen resorption efficiency is similar across stand types. Phosphorus resorption efficiency was highest (76 percent) in recolonized stands suggesting that phosphorus resorption is an adaptive strategy to meet phosphorus demand. Conventional indices of leaf nitrogen to phosphorus and nitrogen resorption efficiency to phosphorus resorption efficiency ratios as indicators of nutrient limitations (as used in other terrestrial systems) may not be applicable in disturbed mangroves because of apparent long-term impacts on soil nutrients following pond construction, operation, and abandonment. Recolonized stands exhibited high phosphorus resorption resulting in low phosphorus concentration of senescent leaves and consequently, low phosphorus input of senescent leaves to soil phosphorus pool.
CONCLUSION: This study demonstrated variations in soil nitrogen and phosphorus, leaf nitrogen and phosphorus, leaf nitrogen and phosphorus ratio, and nutrient resorption efficiencies of nitrogen and phosphorus across stand types and ages. Conventional indices for nutrient limitation of nitrogen and phosphorus using leaf nitrogen to phosphorus and nitrogen resorption efficiency to phosphorus resorption efficiency ratios showed inconsistent indicator of nutrient limitations in mangroves. Hence, a mangrove-specific leaf nitrogen to phosphorus ratio and nitrogen resorption efficiency to phosphorus resorption efficiency ratio are suggested as a more appropriate indicator of nutrient limitation.

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60	5	2

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INTRODUCTION

Nutrient availability (NA) is one of the major factors influencing mangrove forest structure and productivity (Almahasheer *et al.*, 2018). But NA is extremely low in mangrove soils (Kammann *et al.*, 2022). Nitrogen (N) and phosphorus (P) are the primary nutrients often reported to limit mangrove growth (Wei *et al.*, 2023). However, NA varies greatly in mangroves due to soil properties (Adame *et al.*, 2018), tidal inundation, sporadic natural disturbances (Salmo, 2021), and land-use changes (Salvaña *et al.*, 2024). Aquaculture serves as the leading cause of mangrove degradation in Southeast Asia (Contessa *et al.*, 2023). In the Philippines for example, approximately 1,409 hectares (ha) of mangroves were converted to aquaculture ponds from 2000-2020 (Baloloy *et al.*, 2023). The prolonged practice of unsustainable aquaculture has resulted in the neglect and abandonment of numerous ponds (Luo *et al.*, 2022). Abandoned ponds are often highly disturbed environments (Xiong *et al.*, 2021) because of poor soil conditions (e.g., soil excavation, vegetation clearing, and changes in hydroperiod (Salas-Rabaza *et al.*, 2024). The availability of N and P is adversely influenced by these factors, which in turn hampers the growth and development of mangrove seedlings (Chen *et al.*, 2024). Nutrient limitation occurs when the availability of a specific nutrient limits plant growth and productivity (Shi *et al.*, 2024). In natural mangrove stands that are considered to be "nutrient limited", nutrient conservation mechanisms such as nutrient resorption are expected to occur as an adaptation mechanism (Naidoo, 2016). Nutrient resorption refers to a mechanism by which plants conserve nutrients, facilitating the transfer of these essential elements from senescent leaves to other parts of the plant. Globally, terrestrial plants have wide variations in both nitrogen resorption efficiency (NRE), mean at 50 percent (%) and phosphorus resorption efficiency (PRE), mean at 52% (Aerts and Chapin, 1999). But in mangroves (e.g., *Avicennia marina*), NRE and PRE varied widely at 19%-71% and 31%-72%, respectively (Almahasheer *et al.*, 2018). Conventional methods for assessing nutrient limitation typically use terrestrial-based indices, such as the leaf nitrogen: phosphorus (N:P) ratio (Güsewell, 2004) and NRE:PRE ratio (Du *et al.*, 2020). Nevertheless, these indices might not be appropriate for mangrove ecosystems, which are subject to a diverse array of environmental conditions and disturbances. In 2021, the United Nations initiated the Decade of Ecosystem Restoration, aiming to rehabilitate 350 million ha of degraded ecosystems by 2030 (United Nation General Assembly, 2019). Most nutrient-related studies evaluating the benefits of mangrove restoration have focused on carbon accumulation (Ariyanto and Pringgenies, 2024) but rarely assessed changes in NA (Silva *et al.*, 2024). Although there are some studies on NA and resorption efficiencies on mangroves, these are limited to natural stands (Shi *et al.*, 2024; Almahasheer *et al.*, 2018) but rarely account nutrients in restored and recolonized stands. Analyzing nutrient dynamics and contrasting these among natural, restored, and recolonized mangrove stands is crucial for evaluating the stability and recovery of these ecosystems. Classic successional models suggest that mangroves are steady-state ecosystems (Lugo, 1980), but due to periodic disturbance-recovery cycle, it is also considered a successional ecosystem (Odum 1969) with profound cohorts of ages (referred to as "chronosequence" (Jimenez and Lugo, 1985). Studies on the chronosequence of restored planted stands, referred to as "RES" stands, indicates that over time, the structural characteristics of the vegetation can come to closely resemble those of natural forests (Wang'ondu et *al.*, 2014). As mangrove forests mature, increases in soil carbon (Bourgeois *et al.*, 2024) and nutrients are commonly observed (Adame *et al.*, 2018). In recolonized stands (hereon, "COL" stands), where mangroves naturally grow in abandoned ponds, nutrient recovery may be possible through the restoration of tidal flows. The dynamics of tidal flows enable the movement of sediments and nutrients into the ponds, which is essential for the ongoing recovery of mangrove forests (Sidik *et al.*, 2021). Although there is some knowledge regarding the interplay between forest structure, age, and nutrient dynamics in natural mangrove ecosystems, research focusing on the chronosequence of restored and recolonized ponds remains relatively scarce. Understanding nutrient dynamics in restored and recolonized mangroves is fundamentally dependent on this knowledge. This study provides insights on the varying nutrient status and nutrient conservation strategies by investigating changes in soil and leaf N and P, leaf N:P ratio, NRE, PRE, and NRE: PRE ratio across a chronosequence of RES and COL stands (with NAT stands as reference

sites). The hypothesis posits that 1) the levels of nutrients in both soil and leaves are expected to rise with the age of the stand, attributed to enhanced vegetation and soil quality, and 2) nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE) are anticipated to be greater in restored and recolonized stands compared to natural stands. These values were then compared with intact natural mangroves (hereon, "NAT" stands) as the reference system. This study aims to investigate the changes in soil and leaf nutrient concentrations of nitrogen and phosphorus, leaf N:P ratio, nitrogen and phosphorus resorption efficiencies, and nitrogen resorption efficiency:phosphorus resorption efficiency ratio across a chronosequence of restored and recolonized stands. Fieldworks were carried out in the mangrove forest of Ormoc Bay, mid-eastern Philippines in 2022 to 2023.

MATERIALS AND METHODS

Site information

The mangrove forest in Ormoc Bay is a mixture of restored 'planted' (RES), recolonized abandoned ponds (COL), and natural/intact (NAT) stands receiving sediment and freshwater inputs from Bao River (Fig. 1). RES stands (approximately 5-, 8-, and 30-year [y] old, hereon as R5, R8, and R30) are dominated by *A. marina* species except for the 15-y stands (R15) that are dominated by *Sonneratia alba*. COL stands (approximately 5-, 12-, and 20-y old, hereon as C5, C12, and C20) are naturally recolonized with mixed species of mangroves. Waterways (C5) and dikes either intact (C12) or partially-destructed (C20) were observed in COL stands (Table 1). Ormoc climate is characterized by temporal rainfall variabilities which peaks in December and can reach up to 580 millimeters (mm) (Corporal-Lodangco and Leslie, 2017).

Mangrove soils and leaves collection

To determine soil organic carbon (SOC) and nutrients, soil cores were sampled using an open-faced auger (6.5 centimeters [cm] diameter) at 10 cm depth. At each designated plot, two adjacent cores were collected during low tide to assess 1) soil organic carbon (SOC) levels and 2) concentrations of soil

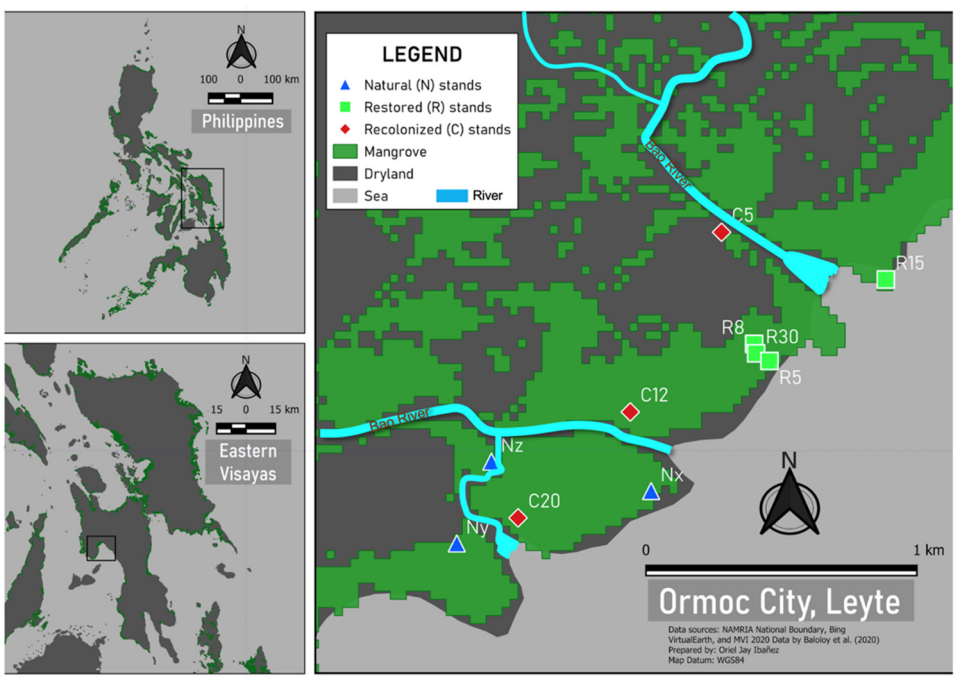


Fig. 1: Geographic location of the study area in Ormoc, Leyte, Philippines
Natural stands (blue triangle), Restored stands (green squares), and Recolonized stands (red diamond). Nx (seaward), Ny (midward), Nz (landward) are natural stands; R5 (5 y old), R8 (8 y old), R15 (15 y old), and R30 (30 y old) are restored stands; C5 (5 y old), C12 (12 y old), and C20 (20 y old) are recolonized stands

Table 1: Vegetation and substrate conditions across stand types and ages in Ormoc mangroves

Parameter	Restored				Recolonized			Natural
	R5	R8	R15	R30	C5	C12	C20	Nx-z
	SW	LW	SW	MW	LW	SW	MW	SW-LW
Vegetation								
Dominant species	*A. marina*	*A. marina*	*S. alba*	*A. marina*	Mixed species			Mixed species
Tree density (ind/ha)	2,249	5,178	1,537	1,732	2,249	4,413	2,858	2,533
Basal area (m^2/ha)	23.75	27.77	18.74	27.69	12.27	17.41	20.02	13.99
Diversity (H')	0.90	0.29	0.90	0.54	1.03	0.19	0.68	1.302
Evenness (E)	0.56	0.21	0.65	0.34	0.64	0.28	0.33	0.51
Dominance (D)	0.47	0.86	0.48	0.75	0.45	0.91	0.73	0.47
Porewater quality								
Salinity (ppt)	28.58±0.25	31.70±1.26	25.86±0.15	28.98±0.67	25.01±0.15	28.54±1.74	29.48±0.29	26.79±1.87
Temperature (°C)	28.80±0.10	29.05±0.11	28.83±0.26	28.68±0.11	28.93±0.26	28.42±0.75	29.38±0.12	29.79±0.45
Redox potential (mV)	-60±05.04	-251.33±21.74	-125.00±09.00	-177.66±33.89	-114.00±15.72	-38.20±6.73	-184.00±15.72	20.03±5.82
pH	5.99±0.29	6.88±0.02	6.43±0.46	6.43±0.46	7.44±0.70	7.45±0.41	6.76±0.03	6.92±0.38

Note: R5 (5 y old), R8 (8 y old), R15 (15 y old), and R30 (30 y old) are restored 'planted' stands; C5 (5 y old), C12 (12 y old) and C20 (20 y old) are naturally recolonized stands. Nx-z are natural stands of unknown ages. SW (seaward), MW (midward), and LW (landward). Based on tidal positions, SW is located at the intertidal zone where mangroves are daily submerged to seawater. MW is located between SW and LW zones. LW is located inland which is approximately 1 kilometer (km) from the shoreline. Porewater quality parameters were measured from each plot using Horiba (U-51, Essex UK)

nutrients. The determination of SOC was conducted using the loss on ignition (LOI) technique (Howard **et al.,** 2014). Each sample was air-dried, oven-dried at 60 degrees Celsius (°C) for 24-48 hours: h (to remove moisture content), and then ignited at 450°C for 4 h (using Neytech Vulcan® muffle furnace). LOI (%) was converted to SOC (%), and corrected for carbonate content by acidification with 1 normality (N) of hydrochloric acid (HCl, J.T.Baker®). Soil samples intended for nutrient analysis were subjected to air-drying for approximately 5 to 7 days, subsequently homogenized, and then finely ground utilizing an agate mortar. Powdered soil samples were forwarded to the Regional Soils Laboratory (Tacloban City, Philippines) for the analyses of total nitrogen (as soil nitrogen [SN]; Dumas-Dry Combustion method (FAO, 2021a), and available phosphorus (as soil phosphorus [SP]; Bray I method (FAO, 2021b). In order to assess leaf nutrient concentrations, samples were gathered from the two predominant mangrove species present in each stand for subsequent nutrient analyses. Around 10-15 leaves from seedlings (hereon as "young leaves") were hand-picked from the first fully expanded leaf after the apical bud. Mature green leaves (hereon as "mature leaves"), devoid of any insect damage or physical injuries, were picked from the 2nd - 3rd internode of the branch from trees, beginning from where the shoots arise. Yellowish senescent leaves (hereon as "senescent leaves") with a well-developed abscission layer (Lovelock **et al.,** 2004) were collected from trees. The young leaves (YNG), mature leaves (MAT), and senescent (SEN) leaves from the triplicate plots were combined to form a composite sample for each leaf stage per stand. Leaf samples were air-dried, oven-dried at 60 °C, then ground to powder. Leaf samples in powdered form were sent to the Central Analytical Services Laboratory located in Baybay City, Philippines, for the determination of total leaf nitrogen (LN) using the Kjeldahl method and leaf phosphorus (LP) concentrations through the vanadomolybdate method, in accordance with the procedures outlined by Motsara and Roy (2008).

Data analysis

Soil nitrogen: phosphorus (Soil N:P) ratio and leaf nitrogen:phosphorus (Leaf N:P) were calculated using mass-based concentrations (Shi *et al.,* 2024). The calculation of NRE and PRE was performed by determining the ratio of the difference in nutrient concentration between mature leaves and senescent leaves, with the results expressed as a percentage (Lovelock *et al*., 2004). Data were tested for normality and homogeneity of variance using the Shapiro–Wilk and Levene's tests. All data were untransformed except for SP values which were log-transformed to conform with the normality test. Data uncertainty was expressed as means ± SEM. One-way analysis of variance (ANOVA) was used to determine differences in soil and leaf nutrient concentrations, leaf N: P, and resorption efficiencies across stand types and ages. Comparison of means was performed with Tukey-HSD post hoc pairwise tests. The data collected from the three natural mangrove stands were pooled since there was no statistically significant difference among stands. Data analysis and visualization were performed using R version 4.2.2 and RStudio version 2023.06.0+421.

RESULTS AND DISCUSSION

Variations of soil nutrients and organic carbon across stand types and ages

SN and SP significantly varied across stand types, ages, and zones within stand types (Fig. 2a-c), $p < 0.05$). RES (0.15±0.01%) and COL (0.18±0.01%) stands have 4% and 27% higher SN than NAT stands (0.14±0.01%; $F = 6.42$, $p < 0.05$), (Fig. 2a). Younger RES (R15: 0.08±0.03%) and COL stands (C5: 0.13±0.01%) had 43% to 7% lower SN than the NAT stands (0.14±0.01%; $p = 0.001$). The SP in RES (8.97±0.74 milligram per kilogram [mg/kg]) and COL (7.05±0.70 mg/kg) stands were 19% and 36% significantly lower than NAT stands (11.10±0.84 mg/kg), (Fig. 2d-f). SP decreased with stand age in RES stands (range: 12.20±1.69 - 6.18 mg/kg), while no distinct pattern was observed in COL stands. SN and SOC values increased from seaward (SW) to landward (LW) in RES stands while SP decreased from SW to LW in COL stands.

The SN (0.16%) and SP (3.58 mg/kg) in COL stands (Fig. 2a-f) were higher than the mean soil nutrient concentrations from natural mangroves in Southeast Asia (range SN:0.02-0.05%; SP: 0.02-25.73 mg/kg), (Table 2). But the SNs (RES: 0.15%, COL: 0.18%, NAT: 0.14%), (Fig. 2a) were higher than those of heavily disturbed mangrove stands (with active shrimp ponds) such as in Todos Santos Bay, Brazil (0.04-0.06%) (Loiola *et al.,* 2023) and planted stands (7-y) in Carey Island, Malaysia (0.04%), (Bakrin Sofawi *et*

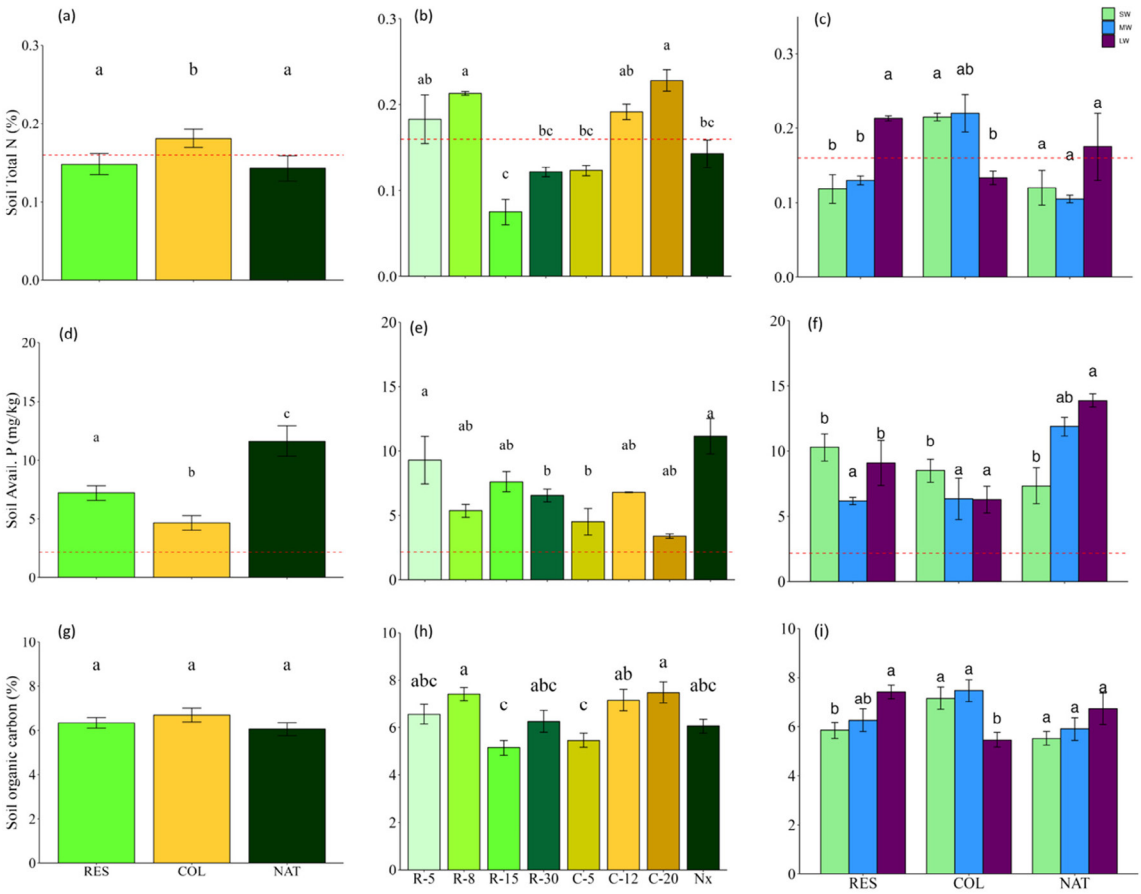


Fig. 2: Soil nitrogen (SN; a-c), available phosphorus (SP; d-f), and soil organic carbon (SOC; g-i) concentrations according to stand types (a,d,g), stand ages (b,e,h), and zonation (c,f,i). Red dashed lines indicate mean SN (0.16%) and SP (3.58 mg/kg) values from natural mangroves in Southeast Asia

al., 2017). In this study, the SPs (RES: 8.97 mg/kg, COL: 7.05 mg/kg, NAT: 11.10 mg/kg), (Fig. 2d) were much lower than the planted (17-, 18-, 50-y) stands in Pangasinan and Bohol, Philippines (mean: 21.56 mg/kg), (Salmo *et al.,* 2013) and active aquaculture ponds in Songkla, Thailand (11.68-102.90 mg/kg (Towatana *et al.,* 2002). The chronosequences of both RES and COL stands did not exhibit a clear SP pattern (Fig. 2d-e). SN concentrations from COL stands increased with stand age, but no distinct pattern was observed from RES stands. Plants absorb essential nutrients from the soil, which are vital for their growth and the synthesis of organic matter. Subsequently, this organic matter is returned to the soil as a result of the decomposition of litter (Sun *et al.,* 2023). In mangroves ecosystems, significant contributions of phosphorus (P) arise from various sources, including litterfall, the mineralization of soil, and human activities such as sewage discharge, agricultural practices, and aquaculture operations (Singh *et al.,* 2015). But because COL stands were once active aquaculture ponds that underwent vegetation clearing (Salvaña *et al.,* 2024), the source of SP is limited. The removal of vegetation, although it allowed for early to mid-vegetation regrowth following the abandonment of the pond, ultimately resulted in a detrimental long-term impact on the soil P pool. The recovery of fauna, especially crabs, plays a significant role in nutrient cycling by facilitating bioturbation processes (Bandibas and Hilomen, 2016). Crab burrowing can alter soil's redox conditions, promoting soil aeration, and N and P availability (Silva *et al.,* 2024). In degraded karst landscapes, an

Table 2: Soil total nitrogen (%) and available phosphorus (mg/kg) from natural mangroves across Southeast Asia

Location	Genus/ species	Soil total nitrogen (%)	Soil available phosphorus (mg/kg)	Sources
Tamsui, Taiwan	*Kandelia candel*	0.2	0.48	Kao and Chang, 1998
		0.13	0.26	
		0.05	1.04	
East Java, Indonesia	-		0.041	Pradipta *et al.,* 2021
			0.027	
			0.032	
			0.039	
			0.043	
			0.032	
			0.038	
			0.021	
			0.029	
			0.032	
			0.038	
Carey Is., Malaysia	*Rhizophora mucronata*	0.027	-	Bakrin Sofawi *et al.,* 2017
Bali, Indonesia	-	0.19	-	Sidik *et al.,* 2019
Pangasinan and Bohol, Philippines	Mixed species	0.18	24.86	Salmo *et al.,* 2013
Trat Province, Thailand	-	-	2.48	Hongwiset *et al.,* 2021
		-	5.96	
Average		0.16	2.17	

improved soil structure and soil nutrients content (C and N) facilitated rapid vegetation succession (Wei *et al.,* 2023; Lu *et al.,* 2022). However, in the semiarid region of China's Loess Plateau, 20 y of afforestation significantly decreased organic carbon and N decomposition rates (Kong *et al.,* 2022). The success of mangrove restoration, akin to that of terrestrial ecosystems, is influenced by multiple factors such as the chronosequence, the techniques employed in restoration, and the unique conditions of the site (Hu *et al.,* 2024). The contrasting nutrient patterns obtained in this study imply the need for more studies to improve the understanding of nutrient dynamics especially in mangroves undergoing recovery.

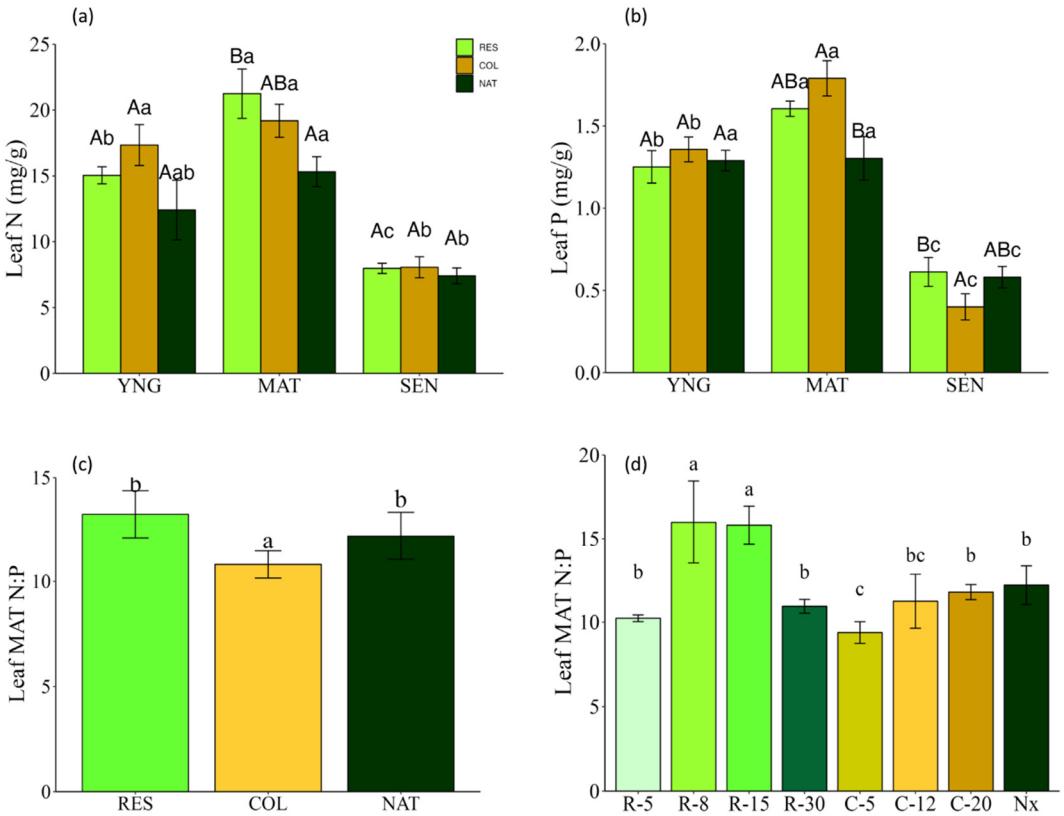


Fig. 3: Leaf N (a) and P concentrations (b) of different leaf stages from different stand types
Leaf N:P ratio of mature leaves according to (c) stand types and (d) stand ages. (a-b) Different capital letters indicate significant differences across stand types of the same leaf stage and lower-case letters represent significant differences between leaf stages at the same stand type (c-d). Different letters indicate significant difference between stand types and stand ages (at α = 0.05; Tukey's HSD test). Young leaves (YNG), mature leaves (MAT), senescent leaves (SEN).

Variations in leaf nitrogen–phosphorus ratios and nutrient resorption efficiencies

The LN and LP concentrations of mature leaves exhibited significant variation among different stand types ($p < 0.05$), (Fig. 3a-b), whereas no such differences were observed in young and senescent leaves. Leaf N: P of mature leaves significantly varied between COL and NAT stands, but not between RES and NAT stands (Fig. 3c). Leaf N:P was relatively stable in different ages in COL stands, but significantly varied among RES stands (Fig. 3d). Mature leaves from RES (21.24±1.87 mg/kg) and COL (20.61±1.24 mg/kg) stands have 39% and 34% higher LN than NAT stands (15.32±1.13 mg/kg; $F = 3.9$, $p = 0.043$), (Fig. 3a). LN and LP significantly increased from young to mature stage, then decreased at senescent stage in all stand types ($p < 0.05$), (Fig. 3a-b).

The LN concentrations of mature leaves in this study (15.32-27.05 milligram per gram (mg/g) (Fig. 3a) were close to the range of values of other mangroves elsewhere (18.52-22.03 mg/g from Jiulong River, southeastern China (Wei *et al.,* 2023); 9.4-10.6 mg/g from Central Red Sea (Almahasheer *et al.,* 2018); 8.4-9.6 mg/g from Palawan, Philippines (Padilla *et al.,* 2004). LP concentrations from these stands (1.30-1.92 mg/g) were 78-96% higher than in natural mangrove forests in the world (0.7 mg/g from Bocas del Toro, Panama (Lovelock *et al.,* 2004); 0.66-0.73 mg/g from Palawan, Philippines, (Padilla *et al.*, 2004), possibly due to an efficient P nutrient resorption strategy. Phosphorus limitation in *R. mangle* has been reported in mature leaves with P concentrations < 0.04 mg/g (Feller *et al.*, 2002). Conversely, the mature leaves examined in various stand types within this study exhibited P

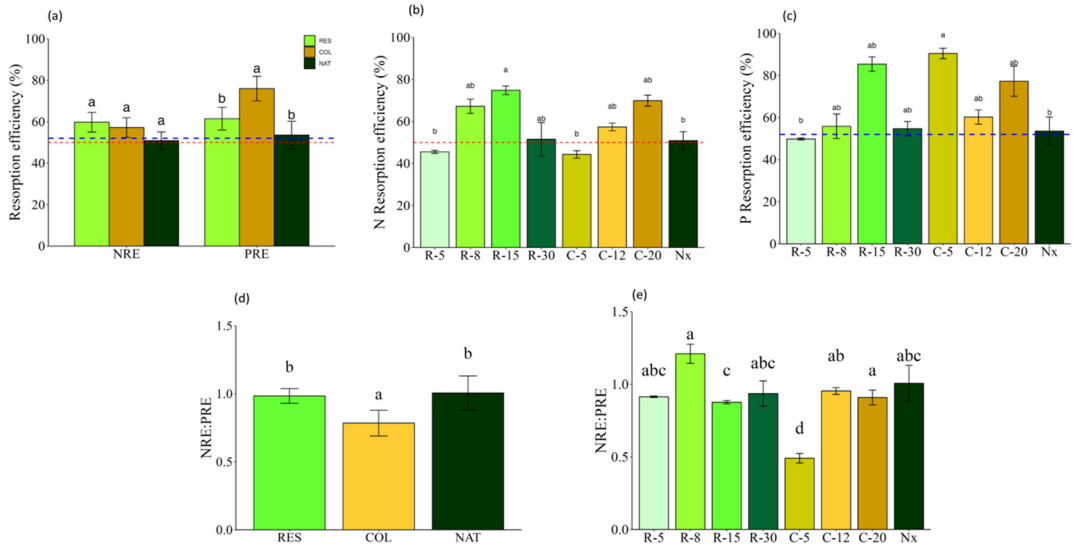


Fig. 4: Nitrogen and phosphorus resorption efficiencies according to (a) stand type, (b-c) stand age, and NRE:PRE ratio according to (d) stand type, (e) and stand ages

Different letters above the error bars indicate a significant difference between stand types or stand ages (at α = 0.05; Tukey's HSD test). Red and blue dashed lines indicate global mean NRE (50%) and PRE (52%).

concentrations that varied between 1.30 and 1.92 mg/g. Although vegetation recovery is apparent in COL stands, senescent leaves contain relatively lower P (Fig. 3b) because of higher resorption (as evidenced by high PRE, 75.99%), presumably to meet plant P demand for survival. The mean N:P ratio (10.8-13.2; Fig. 3c-d) is 20-34% lower than the global mean ratio (16.5), (Tian *et al.,* 2018). The differences observed may stem from the diverse mechanisms of nutrient utilization and cycling that occur among various stand types. The NRE in RES (60%) and COL (57%) stands were higher than the global mean NRE ~50% (Aerts and Chapin, 1999), (Fig. 4a-b), and N in senescent leaves across stand types (7.4-8.7 mg/g) and stand ages (Fig. 3a-b). These values were close to 7 mg/g (Fig. 4a), indicating relative complete resorption of N (Killingbeck, 1996). This indicates that the RES and COL stands may be less efficient in nitrogen conservation, or that the species within these stands do not predominantly depend on N resorption to meet N demand. The PRE in COL stands (76%) were markedly higher than the global mean ~52%, $p < 0.01$ (Aerts and Chapin, 1999), (Fig. 4a-c). P in senescent leaves from COL stands (0.4±0.07 mg/g) was < 0.5 mg/g indicating complete resorption (Killingbeck, 1996). These results imply that species in COL stands are extremely conservative of P. This is a novel evidence for P resorption in disturbed mangroves as observed in the recolonized stands. Complete resorption is common in nutrient-limited environments (Shi *et al.,* 2024) consistent from the *Picea* and *Betula* plantations in Datong County, China where roots mainly absorbed N from soil and P from litter (Liu and Wang, 2021). The fertilization experiment serves as a straightforward approach to assess nutrient limitation (Lovelock *et al*. 2004). Nevertheless, this approach may incur significant expenses, and the meta-analysis did not reveal any clear large-scale trends regarding nutrient limitation (Du *et al.,* 2020). Alternatively, thresholds of leaf N:P ratio (for example, 14:1 versus 16:1 or 10:1 versus 20:1) are widely used to indirectly infer N or P limitation based on the leaf nutrient concentrations (Güsewell, 2004). While these ratios are extensively utilized in terrestrial ecosystems, they were primarily derived from temperate plant species (Sun *et al.,* 2023). In this study, the N:P ratio in mature leaves from all stands was < 14, suggesting a more pronounced N limitation in COL stands (10.8). This situation can be attributed to the long-term consequences of soil excavation that occurred during the construction and subsequent operation of the pond, resulting in a

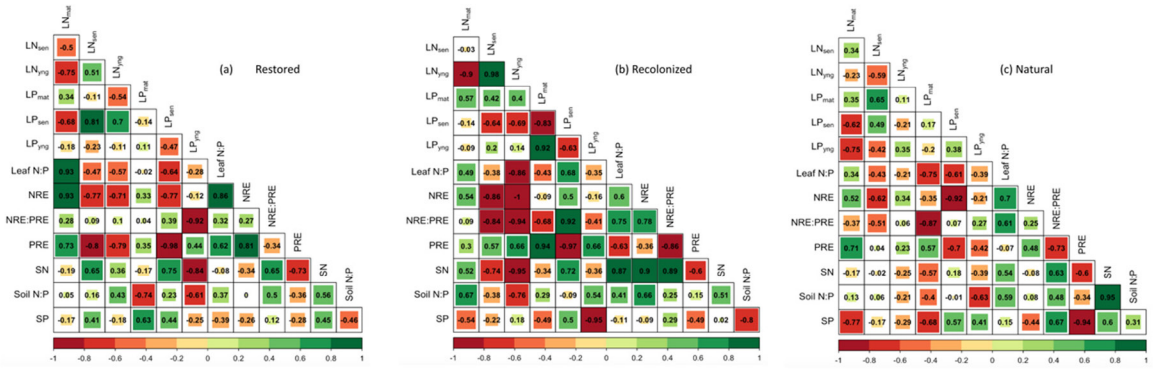


Fig. 5: Heat maps of correlation coefficients between soil and leaf nutrients, leaf nutrient ratios, and nitrogen and phosphorus resorption efficiencies in (a) restored, (b) recolonized, and (c) natural mangrove stands

Note: Significant positive correlations are visualized in blue while significant negative correlations are in red. Color intensities and the sizes of the squares are proportional to the correlation coefficients. LN_{mat} or LP_{mat}, LN_{sen} or LP_{sen}, LN_{yng} or LP_{yng}, NRE, PRE, NRE: PRE, Soil N:P, SN and SP.

diminished N content in the soil. (Adame *et al.*, 2018). Recently, resorption efficiency ratio (NRE:PRE > 1 and NRE:PRE < 1 indicate N and P limitation, respectively) was explored to infer nutrient limitation in mangroves (Shi *et al.,* 2024). However, its dataset focused on terrestrial forest species (Du *et al*., 2020) and may not be directly applicable to mangrove ecosystems, which are characterized by considerable variability in nutrient availability (Alongi, 2020). NRE:PRE ratio was < 1 in both RES (0.98) and COL stands (0.78), suggesting a more pronounced P limitation in COL stands (Fig. 4d-e). Collectively, the use of leaf N:P ratio and NRE:PRE ratio present conflicting N or P nutrient limitation of mangroves in COL stands. Similarly, Wei *et al.* (2023) observed unclear N or P limitation in *Kandelia obovata* stands in China based on leaf resorption efficiency alone. The effectiveness of either the leaf N:P ratio or nutrient resorption efficiency (RE) as indicators of the nutrient status in mangrove species is still uncertain. These findings highlight that leaf N:P ratio (Güsewell, 2004) and NRE:PRE ratio (Du *et al.,* 2020) have the potential to introduce uncertainty in detecting nutrient limitations in mangroves. This may be due to the 1) highly variable environmental conditions in the mangrove ecosystem, and compounded by the 2) long-term/persistent effect of mangrove conversion to aquaculture ponds. In the Philippines, mangroves exist in a variety of stand conditions (natural, recolonized, and restored) based on vegetation structure and the developmental stage (Corcino *et al.,* 2023). These mangroves are also frequently affected by natural and anthropogenic disturbances such as typhoons and conversion to aquaculture ponds (Salmo, 2021). The unique conditions associated with mangrove ecosystems are generally less evident in the majority of terrestrial forests, which may result in their exclusion from the development of the conventional nutrient ratios. Caution should be taken in using these ratios to predict plant nutrient status in mangroves. It is recommended to establish specific indices for the leaf nitrogen to phosphorus (N:P) ratio and the nitrogen resorption efficiency to phosphorus resorption efficiency (NRE:PRE) ratio in mangrove ecosystems to achieve a more accurate assessment of their nutrient status.

Weak correlation between soil nutrient availability and resorption efficiency

Soil nutrient concentrations (SN and SP) were not significantly correlated with leaf nutrient concentrations in all leaf stages (LN or LP; $p > 0.05$) and stand types, nor with resorption efficiency (NRE or PRE). In NAT stands, SP was significantly correlated with PRE (r^2 = -0.94, p = 0.005) while SN was significantly correlated with NRE (r^2 = 0.90, p = 0.014), (Fig 5a-c).

A strong relationship between the nutrient levels in soil and those in leaves was anticipated, given that plants primarily derive their nutrients from the soil (Wei *et al.,* 2023). The results of this study however showed varying weak to moderate correlations between soil nutrient (SN or SP) and leaf nutrient concentrations in all leaf stages across stand types (r^2 = -0.17-0.63, $p > 0.05$), (Fig. 5a-c). This indicates that the concentrations of nutrients in the leaves of mangroves

in Ormoc Bay are not predominantly influenced by soil nutrient levels, suggesting the existence of alternative contributing factors. This contrasts with propositions of direct relationship of mangrove nutrient status with soil nutrients in natural mangroves as observed in the Sundarbans of Bangladesh (Rabiul *et al.,* 2019) and Jiulong River in southeastern China (Wei *et al.,* 2023). The majority of NRE and PRE across stands were not significantly correlated with NA (SN and SP; r^2 = -0.08-0.49, p > 0.05). This observation aligns with findings related to other evergreen species, as the majority of these plants did not exhibit a stable correlation between nutrient RE efficiency and NA availability (Yuan and Chen, 2015). Previous reports on mangroves showed that increasing N availability in soils does not strictly imply an increase in net primary productivity (NPP) and assimilation of extra N (Reis *et al.,* 2017) but instead the need to develop nutrient conservation schemes. Senescent leaves constitute the majority of litterfall in mangrove ecosystems (Pradisty *et al.,* 2022). Leaf litter is a repository of nutrients (Liu and Wang, 2021), and its nutrient ratio affects the quality and rate of nutrient return in ecosystems (Mamidala *et al.,* 2023). In the present study, the N and P concentrations decreased with leaf senescence across stand types (Fig. 3a-b) and stand ages (Fig. 3d), indicating that nutrients were translocated to other parts of the plant before leaf senescence. This expectation arises from the recognition that nutrient resorption serves as a crucial strategy for nutrient conservation, allowing for the recycling of nutrients and minimizing reliance on external sources (Sun *et al.,* 2023). The NRE and PRE of RES and COL stands were significantly higher than NAT stands although COL stands have higher PRE than NAT stands (Fig. 4a-b). Because of the high P resorption in COL and RES stands, it is assumed that the nutrient of senescent leaves, once shedded, contain lower P relative to N. Therefore, leaf shedding would result in the long-term accumulation of N into the detritus matrix as a substantial N pool. Conversely, the process of P resorption during leaf senescence appears to be the primary mechanism for nutrient conservation that addresses the P requirements of mangroves in RES and COL stands. The analysis revealed that there were no significant trends in soil nutrients, leaf tissue nutrient concentrations, or nutrient resorption efficiency in relation to the age of the stand. In RES stands, stand structure differences (i.e. dense monospecific planting in R8, (Table 1) and varying tidal position may strongly influence nutrient variations. A study conducted in the Quanzhou Bay Mangrove Reserve revealed that as the age of restored mangrove stands increases, there is a notable enhancement in soil multifunctionality. This improvement is attributed to the development of microbial communities that are closely linked to N and P cycles (Hu *et al.,* 2024). In contrast, soil inorganic P in a chronosequence of restored mangroves in Guanabara Bay, Brazil does not necessarily increase with mangrove age (Silva *et al.,* 2024). The dense vegetation in R8 and C5 (Table 1) may indicate vegetation recovery, however P resorption is extremely high in COL stands probably as a result of P depletion due to soil excavation and vegetation clearing during pond construction. As a result, leaf litter in COL stands contribute poorly to soil P pool. In COL stands, long-term effects of pond construction (e.g., removal of vegetation, soil excavation) possibly resulted in the alterations of soil recovery including rates and pathways of soil microbial processes which can affect NA (Loiola *et al.,* 2023). Additionally, variations in extractive pressures and the management practices of ponds could account for the discrepancies observed in the age of stands, as well as the concentrations of nutrients in both soil and leaves, along with the efficiencies of nutrient resorption. Differences in tidal water flow (i.e. remnants of large waterways [C5], and dikes that are partially destructed [C20] vs intact [C12]) will either increase/ decrease tidal inundation frequency (Alongi, 2020) and subsequently nutrient input/ output through tidal flushing (Singh *et al.,* 2015). These site-specific differences (rather than stand age) may strongly affect nutrient cycling.

This study highlighted the intricate and dynamic nature of nutrient availability and resorption processes in mangroves that are in the process of recovery. This underscores the need for mangrove-specific leaf N:P ratio and NRE:PRE ratio to better characterize the nutrient status of mangroves. Despite the variability in the rates and trends concerning nutrient availability and resorption, mangrove restoration is positively correlated with improvements in soil multifunctionality, microbial diversity, and abundance of genes associated with N and P cycling (Hu *et al.,* 2024). The beneficial effects linked to the restoration of mangroves can enhance both soil health and the resilience of ecosystems as a whole. Thus, pro-active restoration of mid-to upper-intertidal abandoned aquaculture ponds (Lovelock *et al.,* 2022) is highly suggested to enhance nutrient cycling. Consequently,

this fosters the health and development of mangrove forests, thereby enhancing the overall productivity of the ecosystem. Mangroves are predominantly found in estuarine and bay environments, where significant quantities of N and P-rich sediments are both transported and deposited. Future works can explore how varying levels of N and P affect species diversity (including microbial communities) within mangrove ecosystems, particularly in terms of competition and succession dynamics to understand broader ecosystem implications.

CONCLUSIONS

This study represents the first report on nutrient availability and resorption for Philippine mangroves in chronosequence of restored and natural recolonization stands. The study investigated the changes in soil and leaf N and P, leaf N:P ratio, and NRE:PRE ratio across a chronosequence of RES and COL stands (with NAT stands as reference sites). In contrast to classic successional models, soil nutrients (N and P), leaf tissue nutrient (N and P) concentrations and nutrient conservation (as nutrient resorption from senescence leaf tissue) strategies showed no discernable patterns with stand age. PRE in COL stands, recorded at 76%, exceeds the global average of approximately 52%, indicating that species within COL stands are extremely conservative of P. This is a novel evidence for P resorption in disturbed mangroves as observed in the recolonized stands. It is a well-established knowledge that nutrients accumulate in mangroves through time. However, despite the importance of understanding nutrient dynamics in mangroves, the generality of this accumulation pattern needs further investigation in chronosequences of RES and COL stands. Mangroves habitats are characterized by a scarcity of nutrients, where N and P serve as the main limiting factors for their growth. Conventional approaches to assess nutrient limitation currently rely on terrestrial-based indices of leaf N:P ratio and NRE:PRE ratios. Nevertheless, these indices may not be relevant to mangrove ecosystems that experience significant variations in environmental conditions and disturbances. In Ormoc Bay, Philippines, mangroves of varying stand types exist, including RES, COL, and NAT stands. The approach taken in this study involved the collection of samples from both soil and leaves to perform analyses of their nutrient content. From the nutrient concentrations, leaf N:P, NRE, PRE, and NRE:PRE were calculated. Quantitatively, the results of the study revealed significant variations in soil N and P, leaf N and P in all leaf stages, leaf N:P ratio, and nutrient RE of N and P across stand types and ages. The RES (0.15±0.01%) and COL (0.18±0.01%) stands have 4% and 27% higher SN values than NAT stands (0.14±0.01%). Younger R15 and C5 stands had 43% to 7% lower SN than the NAT stands (0.14±0.01%). LN and LP of mature leaves significantly varied across stand types which increased from young to mature stage, then decreased at senescent stage. Soil nutrient concentrations (SN or SP) were not significantly correlated with leaf nutrients concentrations in all leaf stages and stand types, nor with resorption efficiency. This implies that the presence of nutrients in the soil does not inherently result in their uptake and storage by plants. The efficiency of nitrogen resorption is notably similar among various stand types. The PRE was highest in recolonized stands suggesting that phosphorus resorption is an important strategy to meet phosphorus demand. However, the high PRE in COL stands results to low P concentration of senescent leaves and low P input of senescent leaves to soil P pool. Leaf N:P ratio (<14 indicates N limitation, >16 indicates P limitation) is widely used to indirectly infer N or P limitation based on the leaf nutrient concentrations. NRE:PRE > 1 and NRE:PRE < 1 indicate N and P limitation which was also explored to infer nutrient limitation in terrestrial systems. NRE:PRE ratio was < 1 in both RES (0.98) and COL stands (0.78), suggesting a more pronounced P-limitation in COL stands. Although leaf N:P ratio and NRE:PRE ratio were commonly applied to infer nutrient limitation (mostly in terrestrial systems), such approaches presented conflicting nutrient status of mangroves in this study. This highlights the need for mangrove-specific leaf N:P ratio and NRE:PRE ratio to better characterize the nutrient status of mangroves. The findings revealed that differences in nutrient availability and nutrient resorption during mangrove recovery can occur at varying rates and patterns (to no discernable pattern). This study provides evidence on the complexity and dynamic nature of nutrient availability and resorption in mangroves undergoing recovery. Subsequent studies ought to delve into the recovery of faunal populations, with particular attention to microbial communities, across a more extensive spatiotemporal spectrum, assessing their functional roles in conjunction with nutrient availability and the recovery processes of mangrove ecosystems.

AUTHOR CONTRIBUTIONS

M.E.B. Gerona-Daga has contributed in the conceptualization, methodology, data collection and organization, analysis, writing, and visualization. R.A. MacKenzie was involved in writing the original draft, reviewing, editing, and funding acquisition. L.G. Sumabat-Dacones was involved in writing the original draft, reviewing, and editing. C.F. Naputo contributed to data collection, writing the original draft, reviewing, and editing. S.G. Salmo III, the corresponding author, contributed in the conceptualization, writing, supervision, project administration, and funding acquisition.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interests regarding the publication of this manuscript. In addition, the ethical issues, including plagiarism, informed consent, misconduct, data fabrication and/or falsification, double publication and/or submission, and redundancy have been completely observed by the authors.

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ABBREVIATIONS

%	Percent
°C	Degrees Celsius
COL	Recolonized stand
cm	Centimeter
C5	5-y naturally recolonized stand
C12	12-y naturally recolonized stand
C20	20-y naturally recolonized stand
ha	Hectares
HCl	Hydrochloric acid
ind/ha	Individuals per hectare
km	Kilometer
Leaf N:P	Leaf nitrogen:phosphorus ratio
LN	Leaf nitrogen
LN_{mat}	Leaf total nitrogen of mature leaves
LN_{sen}	Leaf total nitrogen of senescent leaves
LN_{yng}	Leaf total nitrogen of young leaves
LOI	Loss on ignition
LP	Leaf phosphorus
LP_{mat}	Leaf total phosphorus of mature leaves
LPsen	Leaf total phosphorus of senescent leaves
LP_{yng}	Leaf total phosphorus of young leaves
LW	Landward
MAT	Mature leaves
mm	Millimeter
m^2/ha	Meter square per hectare

mg/g	Milligram per gram
mg/kg	Milligram per kilogram
mV	Millivolts
MW	Midward
N	Nitrogen
N:P	nitrogen:phosphorus ratio
NA	Nutrient availability
NAT	Natural stands
Nx	Natural stands of unknown age
NRE	Nitrogen resorption efficiency
NRE:PRE	Nitrogen resorption efficiency:phosphorus resorption efficiency ratio
P	Phosphorus
PRE	Phosphorus resorption efficiency
pH	Potential of hydrogen
ppt	Parts per thousand
RE	Resorption efficiency
RES	Restored stands
R5	5-y restored 'planted' stand
R8	8-y restored 'planted' stand
R15	15-y restored 'planted' stand
R30	30-y restored 'planted' stand
Soil N:P	Soil nitrogen:phosphorus ratio
SE	Standard error
SEN	Senescent leaves
SN	Soil nitrogen
SP	Soil phosphorus
SW	Seaward
y	Year
YNG	Young leaves

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