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Multidisciplinary assessment of a restored mangrove ecosystem in Guanabara Bay, Brazil: linking science and conservation

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Abstract Due to their coastal location, mangrove ecosystems are especially susceptible to various human-caused disturbances. These disturbances can result in a loss of original mangrove cover, a decline in biodiversity, and a degradation of their ecological functions. This study examines a restored mangrove area within the Barão de Mauá Natural Municipal Park (PNMBM) in Guanabara Bay, Brazil, two decades after the initiation of a restoration project. We used a multidisciplinary approach, combining remote sensing analyses, assessment of the vegetation structure, and genetic diversity analysis to evaluate this restored mangrove forest. Remote sensing data demonstrated high Normalized Difference Vegetation Index values following the restoration project's completion, indicating the revegetation's success. Exploring the structure of the new forest, we found *Laguncularia racemosa* to be the most abundant species, with a higher density and dominance for adults and seedlings. Conversely, *Avicennia schaueriana* was the least abundant in all areas, indicating a need for species enrichment. Planting age affected the forest structure, suggesting the capacity of this mangrove to achieve a natural maturity state. There was a genetic erosion in *L. racemosa* individuals, both adults and seedlings and low diversity was observed in *A. schaueriana* individuals. The PNMBM mangrove forest has shown remarkable resilience in maintaining its vegetation cover after restoration despite previous deforestation cycles. Moreover, as a young mangrove forest, it will continue to go through successional stages naturally. The loss of genetic diversity could be a concern for long-term survival, highlighting the need for genetic management. Integrating remote sensing, phytosociology, and genetic diversity analyses provided a comprehensive and detailed view of the park's restoration outcome. These results should be used as guidelines for future interventions outlined in this work and can help ensure the resilience and sustainability of any restored mangrove.

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Introduction

Mangroves are salt-tolerant forests that thrive in intertidal wetlands. Despite their relatively limited plant diversity, they harbor a remarkable abundance of aquatic species (Twilley and Day Jr 2012). These critical ecosystems provide valuable services, significantly contributing to coastal protection, human well-being, and cultural heritage (Friess 2016; Friess et al. 2020). However, they face severe anthropogenic threats, primarily driven by habitat loss and degradation. Between 1980 and 2000, 35% of global mangroves vanished, with ongoing annual losses of 2% globally and 3.62% in the Americas (Valiela et al. 2001). Although the loss rate has slowed significantly since 2000, human activities were responsible for 62% of the global mangrove loss by 2016 (Goldberg et al. 2020). Recent global data indicates that human activities resulted in a 72% reduction in mangrove cover between 2000 and 2020. The loss was more significant in the first decade (75%) compared to the second decade (68%) (Contessa et al. 2023).

This rapid decline of wetlands underscores the urgent need for conservation and restoration. There is a potential risk of losing these vital ecosystems entirely within the next century (Valiela et al. 2001; Duke et al. 2007). Their critical role as blue carbon sinks, sequestering an estimated 10–15% of coastal ocean carbon (Alongi 2014), emphasizes this urgency. Brazil boasts the second-largest mangrove area globally (8.5%), distributed across 90% of its coastline (Cintrón-Molero et al. 2023). Brazilian mangrove forests significantly contribute to global biomass and blue carbon storage, representing approximately 8.5% of the global mangrove carbon stocks (Rovai et al. 2022). Therefore, conserving, rehabilitating, and restoring these ecosystems is essential for safeguarding their valuable fauna, flora, and ecosystem services.

In forest restoration and rehabilitation, planting and natural regeneration are the two main methods. Mangrove natural regeneration can occur under suitable conditions, such as proximity to a propagule source and conducive environmental conditions for seedling establishment and growth (Friess et al. 2019). However, natural regeneration can be slow and may take decades to fully recover. Therefore, large-scale restoration often requires active planting to speed up the regenerative process despite its challenging and complex nature (Friess et al. 2019). Local planting initiatives are emerging in various coastal regions of Brazil, and more information is necessary to develop effective strategies. These restoration efforts are crucial, and long-term monitoring is essential for mangrove reestablishment and addressing future challenges in the area. A comprehensive assessment using remote sensing to measure vegetation cover, ecological structure to investigate forest successional stage and maturity, and genetic diversity analysis to ensure long-term persistence of the species can help gauge the restoration success and guide better management practices.

Remote sensing methods play a crucial role in the early detection of mangrove degradation, allowing for intervention to mitigate stressors and preserve the natural successional processes before deforestation sets in (Lewis III et al. 2016). This approach is valuable even in severely degraded areas, monitoring successful reforestation and natural forest recovery. The normalized difference vegetation index (NDVI) serves as an indicator for mangrove disturbance and recovery. It is calculated from the difference between near-infrared and red band reflectance values (Aljahdali et al. 2021). Healthy vegetation absorbs red light and reflects near-infrared light due to chlorophyll and cell structure in the leaves. This results in lower red band reflectance and higher near-infrared band reflection values (Ruan et al. 2022). Consequently, higher NDVI values typically indicate denser and healthier vegetation, which facilitates monitoring changes over time. Since erosion is a leading cause of mangrove loss in Brazil (Goldberg et al. 2020), such time-series monitoring is crucial in preventing further vegetation loss.

Monitoring restored areas is essential to ensure the success of restoration projects and to inform future management decisions. It can help determine if projects are being implemented correctly, performing as expected, and using resources efficiently (Viani et al. 2018; Ferreira et al. 2023). Some studies only use remote sensing to monitor restored areas, evaluating vegetation cover advancement and the efficient occupation of vegetation (Lewis III et al. 2016; Goldberg et al. 2020). However, the effectiveness of mangrove restoration projects must be assessed through methods and protocols that monitor both the increase in vegetation cover and the reestablishment of ecosystem processes, such as productivity, carbon and nutrient dynamics, and sediment dynamics, and the development of the spatio-temporal structure of vegetation (e.g., growth of planted and recruited individuals, recruitment of new individuals, mortality rates) (Cadier et al. 2020; Ferreira et al. 2023). In this regard, phytosociological studies that evaluate the structure of the different strata of the mangrove tree vegetation can be carried out either through rapid sampling methods or through the establishment of permanent plots (Viani et al. 2018). Thus, the data generated by the phytosociological reassessment will allow technicians and managers of these areas to employ management techniques and resources more efficiently, ensuring development and successional advancement, the re-establishment of ecosystem processes, and the success of restoration (Schmitt and Duke 2015; Viani et al. 2018; Ferreira et al. 2023).

The genetic population structure and diversity levels are reliable indicators of gene flow, an important evolutionary force for plants (Ellstrand 2014). Previous genetic analysis of several mangrove areas in Rio de Janeiro state using ISSR and AFLP markers revealed low polymorphism and diversity levels (Lira-Medeiros et al. 2015; Granado et al. 2018). Recent advancements in next-generation sequencing (NGS) provide a more comprehensive view of genetic diversity through SNP markers, aiding reforestation activities, species identification, and adaptation studies (Wee et al. 2019). Among the available NGS methods, multiplexed ISSR genotyping by sequencing (MIG-seq) stands out for its efficiency and cost-effectiveness (Suyama and Matsuki 2015; Suyama et al. 2022). Importantly, MIG-seq eliminates the need for extensive optimization and is applicable in various fields, including ecology, evolution, conservation biology, and agricultural development (Sakaba et al. 2023; Suetsugu et al. 2023a, b; Takahashi and Suyama 2023). This versatility makes it a valuable tool for understanding the interplay between genetic variation and its biological consequences, even in species with limited genetic information.

The Brazilian mangroves are under significant pressure due to factors such as population growth, real estate speculation, and misinformation. Mitigating these difficulties, recent government initiatives such as the “ICMS Verde” environmental tax have helped create and maintain protected areas (Chueiri et al. 2020). In 2012, the municipal government of Magé in Rio de Janeiro state established the Barão de Mauá Natural Municipal Park (PNMBM—“Parque Natural Municipal Barão de Mauá”). The area, which had previously been heavily deforested, received renewed attention after a major oil spill in Guanabara Bay in 2000 (Michel 2000; Santos et al. 2024). A reforestation project was initiated, involving the planting of mangrove seedlings, their monitoring, and educational activities (A. Silva, personal communication). The PNMBM mangrove has been significantly impacted by several events, including deforestation for logging for charcoal production, landfilling for human settlements, natural erosion, and sequential oil spills. All these severe impacts and the social and environmental importance of the area encouraged the carrying out of a restoration project that has been carried out since the 2000s (Santos et al. 2024). After 20 years of restoration of the first areas, it is essential to monitor different components of this vegetation to understand whether the efforts efficiently ensure the mangrove’s reestablishment. To achieve this, we employ an interdisciplinary approach combining time series remote sensing, phytosociological structure assessment, and genetic diversity analysis to investigate the current state of the ecosystem. We believe that the use of a multidisciplinary approach to evaluate different components of restored areas spatiotemporally can generate information that allows the development of more efficient actions for the management, handling, and conservation of threatened ecosystems, such as mangroves, especially for managers, decision-makers, and stakeholders.

Firstly, we analyzed the PNMBM area through image processing and remote sensing analysis. The aim was to measure the vegetation cover progress from 1985 until 2022, from before planting to when planting was over. Since the information about mangrove restoration in several parts of the PNMBM was not accessible, this analysis showed a view of the vegetation loss and gain through time. After that, we focused on a specific area of the PNMBM with known restoration data for phytosociological structure and genetic diversity analyses. Therefore, we investigated the vegetation structure to evaluate the forest’s maturity in different planting ages and the occurrence of seedlings in those areas. We hypothesized that areas planted before would show advanced or intermediary successional stages compared to recently planted areas. Furthermore, we aimed to indicate the minimal time necessary for reforestation monitoring to achieve a mature mangrove forest structure. Then, we investigated the genetic diversity of two mangrove species to evaluate if the restoration process affected it inside the PNMBM. These analyses were examined within each area of expertise and combined to deliver management guidance for this protected area. These results serve as an example for other areas where mangrove forests have been or are being restored, in order to enhance the effectiveness of these activities on a global scale.

Materials and methods

Study area

The Barão de Mauá Natural Municipal Park (PNMBM) was established in 2012 to protect an area of 115.7 hectares in the northwest region of Guanabara Bay, Magé, Rio de Janeiro state, Brazil (Fig. 1). This protected area serves as a barrier against real estate speculation and unsustainable use, preserving the region's natural heritage. The park is located at geographic coordinates 22° 43′ S and 43° 11′ W, within a tropical climate with temperatures ranging from 17 to 31 °C and an average annual rainfall of 1450 mm (CLIMATEMPO 2023). It falls within the Atlantic Forest Biome, which is recognized as a

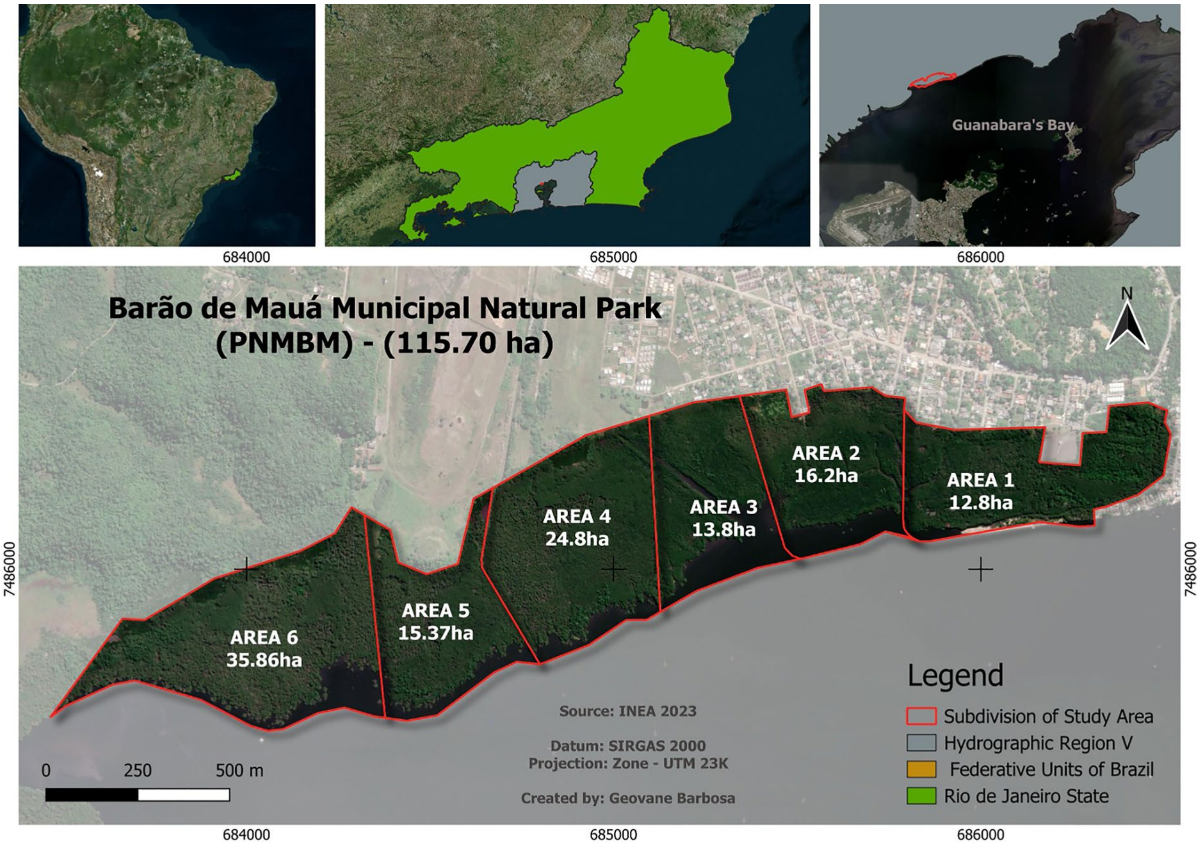


Fig. 1 Maps showing the location and restoration areas of the Barão de Mauá Natural Municipal Park (PNMBM). The top maps depict a zoomed-in view of Brazil (in yellow), the state of Rio de Janeiro (in green), and the Guanabara Bay region (in grey). The bottom map provides an aerial view of the PNMBM, highlighting six restoration areas designated in 2001 by the OndAzul Institute. The names and sizes (in hectares) of these areas are indicated. Created by Geovane Barbosa

global biodiversity hotspot (Myers et al. 2000; Mittermeir et al. 2005).

The mangrove restoration project, organized by the OndAzul Institute, involved dividing the planting areas into six numbered sections (Areas 1 to 6 in Fig. 1). The OndAzul Institute initiated its restoration efforts by restoring the hydrological system and transplanting and planting trees in Area 1 (Santos et al. 2024). Meanwhile, other projects began planting in Areas 4 to 6, while the OndAzul Institute sequentially worked on Areas 1 to 3. Information regarding the origin of propagules and planting in Areas 4 to 6 was not available, so the phytosociological and genetic studies presented in this document focused on Areas 1 to 3, for which information was accessible. Planting in Areas 1, 2, and 3 commenced in 2003 and was completed in 2016. Consequently, Area 1 is approximately 21 years old, Area 2 is 13, and Area 3 is 11.

Guanabara Bay's mangrove forests consist of three native species: *Laguncularia racemosa* (L.) C. F. Gaertn., *Avicennia schaueriana* Stapf & Leechm. ex Moldenke, and *Rizophora mangle* L. All three species were used in the restoration efforts, with planting methods adapted to the specific conditions of the bay. Factors such as tidal inundation, salinity, and substrate composition were taken into consideration. In certain areas, a planting mix that included all three species was used to improve the resilience and biodiversity of the restored mangroves.

Specimens of the three species found in PNMBM were collected and deposited in the Herbarium Collection at the Rio de Janeiro Botanical Garden (RB) with the following accession numbers: RB834782 (*A. schaueriana*); RB834783 (*L. racemosa*); RB834781 (*R. mangle*).

Image processing and remote sensing analysis

A geospatial temporal analysis of the PNMBM area was conducted using satellite images provided by the United States government, the European Union, and NASA from 1984 to 2022. This allowed for a visualization of historical changes in the mangrove forest cover within Guanabara Bay.

The analyses employed Landsat satellite imagery, using Landsat 5 sensor data from 1985 to 2011 and transitioning to Landsat 7 sensor data from 2012 to 2022 (land remote sensing satellite program (LANDSAT), image courtesy of the U.S. Geological Survey). The image acquisition and Normalized Difference Vegetation Index (NDVI) analysis were performed on the Google Earth Engine platform using images with a maximum of 10% cloud cover and a 30 m spatial resolution. Bands 4 (Near Infrared—NIR) and 3 (Red) were used to calculate the NDVI using the following formula:

$$\mathrm{NDVI} = \frac{\mathrm{NIR} - \mathrm{Red}}{\mathrm{NIR} + \mathrm{Red}}$$

The QGIS software offers advantages for various geospatial data processing tasks, moreover being free and open-source allows for user contributions and continuous improvement (Falcão et al. 2005). Therefore, for this study, post-processing and analysis were conducted using QGIS 3.28 software (QGIS Development Team 2023). It was used to generate time series maps and perform zonal statistical analysis for the study years. The statistical analysis yielded minimum, maximum, mean, standard deviation, and variance values, which were exported in xlsx format and further analyzed in Microsoft Excel.

Phytosociological survey and analysis

In order to assess the population structure of *A. schaueriana*, *L. racemosa*, and *R. mangle* in the PNMBM restoration areas, we set up a total of 60 plots, each measuring 100 m² (4×25 m). Within these 60 plots, 20 were designated for each of the three studied areas (Areas 1, 2, and 3). The plots were positioned perpendicular to a transect running from the estuarine edge to the transition with houses (Schaeffer-Novelli and Cintron-Molero 1986; Rovai et al. 2021).

We placed 5 plots as replicates within 4 zones along the transect, ensuring that the spatial orientation remained parallel to the bay's coast. This replication of plots enhanced sampling robustness and allowed for a representative depiction of the studied area, taking into account the mangrove flooding gradient and zonation.

Within each plot, all individuals taller than 1.3 m were identified, measured, and considered adults for this study. The measurements included visually estimated height and diameter at breast height (DBH) taken 1.3 m above the ground. For seedling sampling, five subplots of 1 m^2 each were spaced 5 m apart along the central line of each 100 m^2 plot. All individuals within these subplots with a height of less than 1.2 m were classified as seedlings. Seedling data included species identification and counting, and height and diameter at base height (DAB) measurements. All measurements followed guidelines by Schaeffer-Novelli and Cintron-Molero (1986) and Balke et al. (2013).

We calculated abundance (n), relative density (DeR%), height (H), relative dominance (DoR%), and basal area (g) (Schaeffer-Novelli and Cintron-Molero 1986; Moro and Martins 2011). Adult data analysis included calculating these parameters for: (a) each area, regardless of species, (b) each species, regardless of area, and (c) each combination of area and species. Seedling data analysis only included n, DeR%, and H. A multifactorial analysis of variance (ANOVA) was conducted to test for significant differences in adult and seedling abundance. This ANOVA considered the factors of area, species, and their interaction.

We used various statistical analyses to assess and compare the population structure of different mangrove species across the three restored areas. First, we created frequency distribution tables based on size classes derived from phytosociological parameters (Sturges 1926). These tables provided a visual representation of the population structure within each area. We calculated the minimum, maximum, and average values for height and DBH data. To evaluate significant differences in height and DBH between species and across the three areas, we employed non-parametric Kruskal-Wallis rank sum tests. Levene's test confirmed that our data did not follow a normal distribution, justifying the use of this non-parametric test. The analyses were conducted using R packages within RStudio (R Core Team 2023) on the Posit. Cloud platform: easyanova (Ritter et al. 2019), TukeyHSD (Ritter et al. 2019), dplyr (Wickham et al. 2023), dunn.test (Dinno 2017), and pacman (Rinker and Kurkiewicz 2018).

Genetic diversity analysis

We aimed to study the genetic structure of all three species from PNMBM. We successfully obtained DNA samples from *L. racemosa* and *A. schaueriana*. However, we encountered difficulties in obtaining good-quality DNA from *R. mangle*. Despite trying various DNA extraction protocols and kits, the DNA yield was insufficient, and the solution was viscous due to polysaccharide contamination. Consequently, the PCR amplification was poor and unsuitable for sequencing *R. mangle* samples with MIG-seq methodology.

Additionally, some DNA samples of *L. racemosa* and *A. schaueriana* from Area 1 used in this work were already available in our laboratory from previous studies. These samples were collected in 2014 from remnant autochthonous plants originally from that area (REM) and allochthonous plants used at the beginning of the restoration (PL) (details in Granado et al. 2018). Unfortunately, we had no DNA samples of *R. mangle* from that time due to the aforementioned problems. We then decided to exclude the *R. mangle* from the genetic diversity analysis, as we believed it would not compromise our interdisciplinary analysis of the PNMBM.

In 2021 and 2022, we collected fresh leaf samples from 48 individuals of *L. racemosa* and *A. schaueriana* each. The individuals were spaced at least 50 m apart to reduce spatial autocorrelation, since most of them were collected in different plots during the phytosociological survey. We sampled 8 adults and 8 seedlings from each area. The samples were meticulously stored in silica gel to preserve DNA integrity for extraction. The total DNA samples analyzed with MIG-seq sequencing were as follows: 8 REM, 8 PL, 24 Pl, and 24 Sl.

The DNA extraction followed the protocol described by Lira-Medeiros et al. (2015). Quantification was carried out using a Nanodrop 2000 (ThermoFisher), and the integrity was confirmed through 1% agarose gel electrophoresis. For the MIG-seq sequencing, the protocols described by Suyama et al. (2022) with primer set-1 and Suyama and Matsuki (2015) were utilized. The PCR temperature was optimized, incorporating purification/equalization steps and removal of short fragments (<250 bp) using AMPure XP. Sequencing was conducted on an Illumina MiSeq platform using the MiSeq Reagent Kit v3 (150 cycles). The paired-end and index sequencing covered both fragment and index ends. The "Dark-Cycle" option was adjusted to exclude the initial 17 bases (SSR and anchor regions) in both reads, resulting in effective read lengths of 80 bases for each.

Following Suyama and Matsuki (2015), the forward and reverse reads of each sample were merged. Low-quality reads were eliminated using

Trimmomatic v.0.32 (Bolger et al. 2014) with the specified commands: HEADCROP:6, CROP:77, SLIDINGWINDOW:10:30, and MINLEN:51. The obtained reads were assembled using the Stacks v.2.41 pipeline (Rochette et al. 2019). The minimum depth was set to 6 (−m 6), and default values were employed for the other options. Subsequently, a population program in Stacks was used to extract single nucleotide polymorphisms (SNPs) with a genotyping rate exceeding 80%. Loci with observed heterozygosity greater than 0.6 and SNPs with minor allele count less than 3 were excluded to remove paralogous loci and possible PCR errors. Additionally, highly linked SNPs showing R^2 greater than 0.4 were excluded using PLINK v1.90 (Chang et al. 2015).

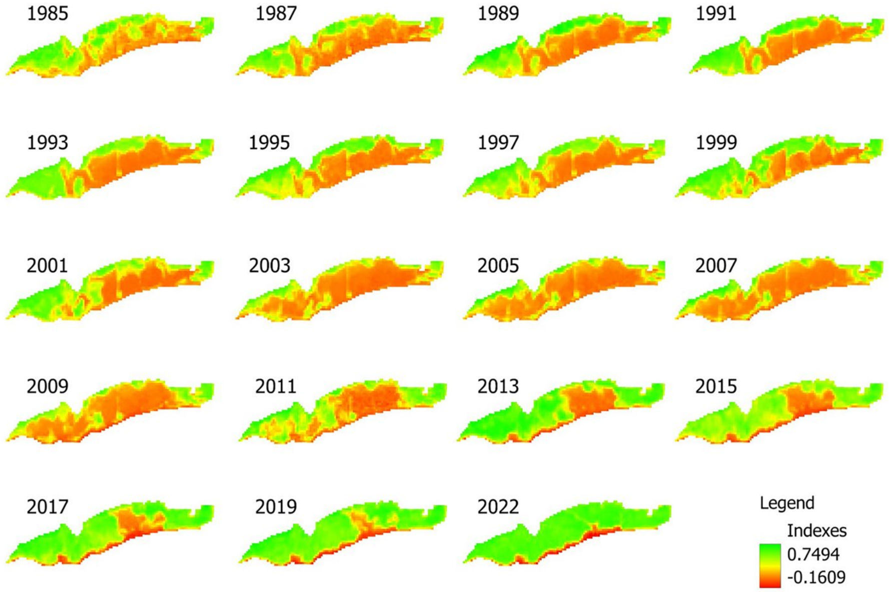
Genetic analyses of the SNP markers were conducted using the Posit Cloud platform for RStudio software (R Core Team 2023). The following packages were utilized: adegenet v.2.1.10 (Jombart and Ahmed 2011), ade4 v.1.7–22 (Dray and Dufour 2007) and factoextra v.1.0.7 (Kassambara and Mundt 2020). These packages were employed to calculate genetic diversity indices, such as observed heterozygosity (Ho) and expected heterozygosity (He), perform a discriminant analysis of principal components (DAPC), an analysis of molecular variance (AMOVA), and Bartlett's test of homogeneity of variances. DAPC is a multivariate method that partitions genetic variation into a between-group and a within-group component, maximizing the former while minimizing the latter (Jombart et al. 2010), which is suitable for groups of data with low genetic variance.

Results

Remote sensing

The mangrove area at PNMBM started degrading in the 1980s. Satellite imagery from 1985 confirms extensive degradation by that time. The deforestation and changes in the area's hydrological and physical conditions intensified after a major oil spill in Guanabara Bay in 2000, and most of the vegetation was lost at the PNMBM (Fig. 2; Supplemental Material 1). The restoration project in Area 1 of the PNMBM, carried out by the OndAzul Institute, began in 2001. It wasn't until 2007 that the environmental rehabilitation efforts started showing results, with a slight expansion of vegetation cover on the park's right side (details in Santos et al. 2024; see Fig. 2). By 2013, the restoration efforts in Areas 4 to 6 on the left side of the park (see Fig. 1) had achieved full recovery. Concurrently, the vegetation cover achieved in Area 1 spread to Area 2 and eventually to Area 3 due to planting and monitoring. The planting phase concluded in 2016, and there was continuous recovery of vegetation, leading to

Fig. 2 Maps illustrating the temporal series of NDVI analysis (1985–2022) for the mangrove restored area at Barão de Mauá Natural Municipal Park (PNMBM)



complete cover by 2022 by natural regeneration (Fig. 2; Supplemental Material 1).

The mangrove forest cover in the area has successfully rebounded after more than 40 years of degradation and regeneration cycles. Geostatistical analysis using the NDVI revealed historically low vegetation cover in the studied area, where Area 6 had the highest values (Fig. 3). There was a notable decrease in vegetation cover between 2001 and 2003 due to oil contamination. 2003, active planting efforts began in the PNMBM, resulting in relatively stable but low vegetation levels until 2008. After 2008, the average NDVI showed a positive trend, reaching its peak in 2022 (Fig. 3).

Phytosociological analysis in the PNMBM

Area-level analysis

The phytosociological studied the plant communities within the three designated restoration areas (Areas 1 to 3) in the PNMBM. The area-level analysis compared the abundance, density, basal area, dominance, and height of adult trees and seedlings across all three areas (Table 1).

Adults

Area 1 had the lowest number of adult trees ($n = 515$), while Area 2 had the highest number ($n = 951$), followed by Area 3 ($n = 815$). This difference was statistically significant ($df = 2$, $F = 3.124$, $p < 0.05$). Interestingly, Area 1 had the highest

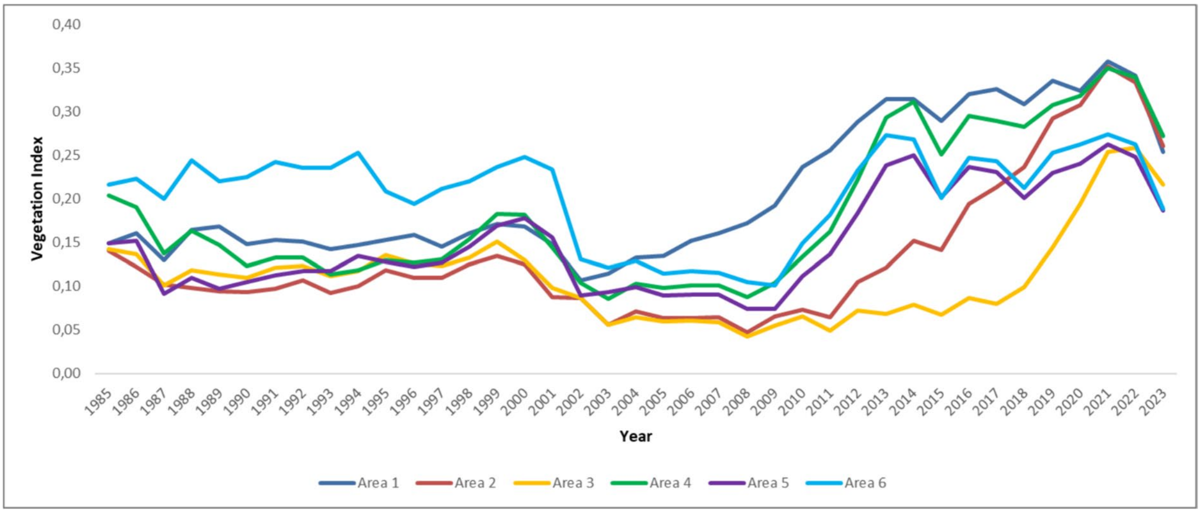


Fig. 3 Graphic showing the yearly vegetation index, from 1985 to 2023, for all six areas of restored mangrove in Barão de Mauá Natural Municipal Park (PNMBM)

Table 1 Overall data for adult trees and seedlings within the PNMBM restoration Areas 1, 2, and 3, including abundance (n, number of individuals), relative density (DeR, percentage), basal area (g, $m^2\ ha^{-1}$), relative dominance (DoR, percentage), and height (H, meters with standard deviation)

	Area	n	DeR (%)	g ($m^2\ ha^{-1}$)	DoR (%)	H (m)
Adults	1	515^{a}	22.58	7.62^{a}	50.29	4.47 (±1.23)^{a}
	2	951^{b}	41.69	3.77^{b}	26.04	3.66 (±1.16)^{b}
	3	815^{b}	35.73	3.59^{b}	23.68	3.79 (±1.39)^{c}
Seedlings	1	678^{a}	45.23	–	–	0.29 (±0.22)^{a}
	2	444^{a}	29.62	–	–	0.24 (±0.17)^{b}
	3	377^{a}	25.15	–	–	0.19 (±0.13)^{c}

Superscript letters (a, b, c) indicate significant differences between areas in ANOVA relative dominance (50.29%) of adult trees but the lowest relative density (22.58%). The relative densities and dominances of adult trees in Areas 2 and 3 were similar (Table 1). Thus, although Area 1 had fewer adult trees, they were larger and contributed more to the overall tree cover. Moreover, Area 1 displayed a significantly higher basal area (7.62 m^{2}ha^{-1}), which was almost double that of Areas 2 and 3 ($df=2$, $F=149.72$, $p<0.0001$). In addition, tree height was significantly different among the areas. The average height was tallest in Area 1 compared to Areas 2 and 3 ($df=2$, $F=91.31$, $p<0.0001$) (Table 1).

Seedlings

In our study, we found that Area 1 had the highest number of seedlings ($n=678$) and the highest relative density (DeR = 45.23%), while Area 2 had the lowest number of seedlings ($n=444$) and a relative density of 29.62%. There were no statistically significant differences in the abundance of seedlings among the three areas ($p=0.339$). However, we observed significant differences in the mean seedling height between the areas, with the tallest average in Area 1 and the shortest in Area 3 ($df=2$, $F=45.513$, $p<0.0001$) (Table 1).

Species-level analysis

The second approach to analyzing the vegetative structure involved studying adult trees according to their species and location. This analysis revealed interesting patterns related to abundance, relative density, basal area, relative dominance, and height (Table 2). It also examined seedlings based on abundance, relative density, and height (Table 3).

Adults

In the study area, *L. racemosa* was the most dominant species with 1296 individuals (DeR = 56.3%), followed by *R. mangle* with 911 individuals (DeR = 40.4%) and *A. schaueriana* with 74 individuals (DeR = 3.3%). These differences were statistically significant ($df=2$, $F=18.135$, $p<0.0001$), and *A. schaueriana* had significantly lower density compared to the other two species ($p<0.001$) (Table 2).

Laguncularia racemosa also had the largest basal area and relative dominance, followed by *R. mangle* and *A. schaueriana*. The differences in basal area among the three species were statistically significant ($df=2$, $F=18.135$, $p<0.0001$), with pairwise comparisons also significantly different ($p<0.001$ for all pairs) (Table 2). Additionally, analysis of the basal area distribution revealed a "J-inverted" curve for *L. racemosa* and *R. mangle* in all areas (Fig. 4),

Table 2 Species and area-specific population structure of adult trees in the PNMBM restoration project, including abundance (n, number of individuals), relative density (DeR, percentage), basal area (g, m^{2}ha^{-1}), relative dominance (DoR, percentage), and height (H, meters with standard deviation)

Espécies	Área	*n*	DeR (%)	g (m^2.ha^{-1})	DoR (%)	H (m)
Av	1	49^{a}	2.15	0.869^{a}	5.73	4.31 (± 1.38)^{a}
	2	4^{a}	0.18	0.076^{b}	0.5	6.28 (± 0.85)^{a}
	3	21^{a}	0.92	0.144^{c}	0.95	3.48 (± 1.23)^{a}
	Total	74^{A}	3.3	2.0^{A}	6.0	3.21 (± 1.23)^{A}
Lg	1	284^{a}	12.45	5.438^{a}	35.87	4.73 (± 1.07)^{a}
	2	$345^{a,b}$	15.13	2.750^{b}	16.99	4.41 (± 0.93)^{b}
	3	667^{b}	29.24	3.344^{b}	22.06	4.05 (± 1.34)^{b}
	Total	1296^{B}	56.3	23.5^{B}	70.6	2.58 (± 2.24)^{B}
Rh	1	182^{a}	7.98	1.316^{a}	8.68	4.14 (± 1.32)^{a}
	2	602^{b}	26.39	1.121^{b}	7.4	3.20 (± 1.03)^{b}
	3	127^{a}	5.57	0.101^{c}	0.67	2.44 (± 0.67)^{a}
	Total	911^{B}	40.4	7.8^{C}	23.4	2,29 (± 1.64)^{C}

Av *Avicennia schaueriana*, Lg *Laguncularia racemosa*, Rh *Rhizophora mangle*

Lowercase letters represent differences in populations of each species when areas are compared, while uppercase letters represent differences between species

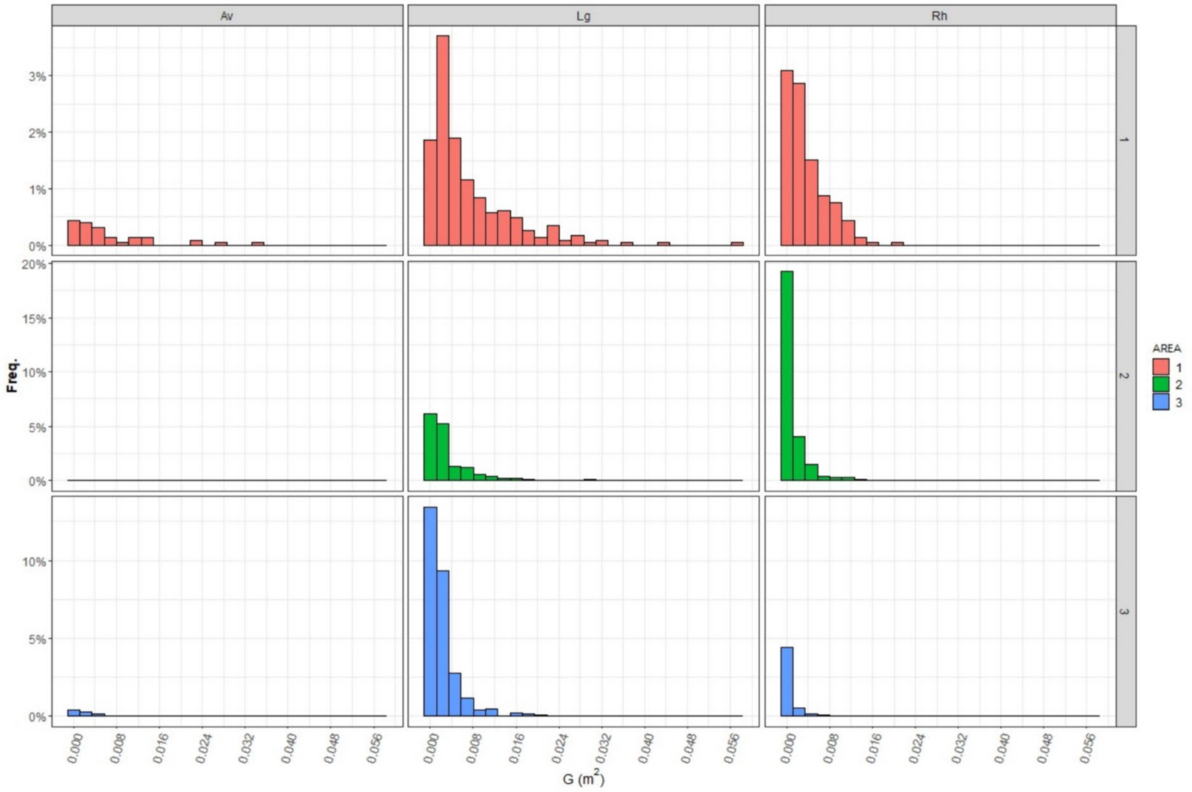


Fig. 4 Frequency graph showing basal area classes for the three species (vertical grids) in Areas 1, 2, and 3 (red, green and blue, respectively; horizontal grids). Av *Avicennia schaueriana*, Lg *Laguncularia racemosa*, Rh *Rhizophora mangle*

indicating a predominance of younger individuals in these species.

Avicennia schaueriana had the highest average height, while *R. mangle* had the lowest. All three species showed statistically significant differences in average height (df = 2, F = 14.365, $p < 0.0001$), with pairwise comparisons showing significant differences ($p < 0.05$ for all pairs). The height distribution across classes (Fig. 5) demonstrated a concentration of individuals in intermediate height classes. *Laguncularia racemosa* predominantly had individuals between 3 and 5 m, while *R. mangle* had a majority within the 1- to 4-meter range. *Avicennia schaueriana* displayed minimal variation across height classes.

Avicennia schaueriana

Avicennia schaueriana showed the lowest abundance and relative density across the areas, with the highest values in Area 1 and the lowest in Area 2. However, there was no statistically significant difference in abundance between the areas (p = 0.083). Basal area and relative dominance followed a similar pattern, with the highest values in Area 1. The three areas differed significantly in basal area (df = 2; F = 5.856, p = 0.004), with pairwise comparisons showing significant differences ($p < 0.05$ for all pairs). Consistent with the other species, *A. schaueriana* individuals primarily belonged to smaller basal area classes (Fig. 4). The average height of *A. schaueriana* was the highest in Area 2 but there was no significant variation between the three areas (p = 0.119) (Table 2). The distribution of heights across classes did not reveal a clear pattern (Fig. 5).

Laguncularia racemosa

In our study, we found that *L. racemosa* was the most abundant adult tree species. Its abundance and density in Area 3 were larger than in Area 1 and Area 2, and these differences were statistically significant (df = 2; F = 5.396, p = 0.007). Further analysis revealed that only Area 3 differed significantly from Area 1 in pairwise comparison (*p* = 0.007). When it

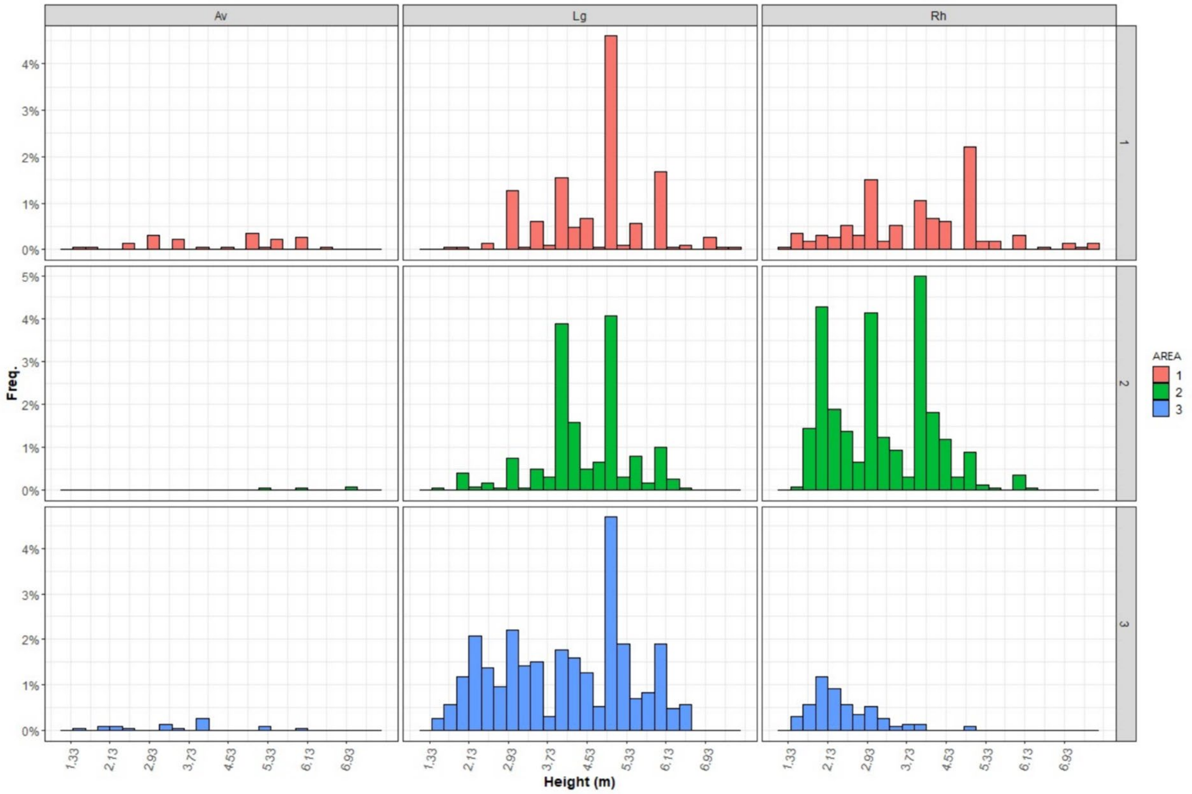


Fig. 5 Frequency graph showing height classes for the three species (vertical grids) in Areas 1, 2, and 3 (red, green and blue, respectively; horizontal grids). Av *Avicennia schaueriana*, Lg *Laguncularia racemosa*, Rh *Rhizophora mangle*

comes to basal area and relative dominance, the highest values were observed in Area 1, and all areas showed significant differences in basal area (df = 2; F = 26,540, p < 0.001), whereas Area 1 differed significantly from the other two areas (p = 0.001 for pairs A1:A2 and A1:A3). Analysis of basal area distribution revealed that most *L. racemosa* individuals fell within lower-size classes (Fig. 4). Once again, Area 1 had the largest individuals, and there were significant differences observed between the three areas (df = 2; F = 13.514, p < 0.001). Area 1 differed significantly from the other two areas (p = 0.001 for pairs A1:A2 and A1:A3) (Table 2). The distribution in height classes showed a concentration of *L. racemosa* individuals at intermediate heights in all three areas (Fig. 5).

Rhizophora mangle

The abundance of *R. mangle* was highest in Area 2 and lowest in Area 3. There were significant differences between the areas (df = 2; F = 9.240, p < 0.001), with Area 2 significantly differing from Areas 1 and 3 (p < 0.01 for pairs A2:A1 and A2:A3). Basal area and relative dominance were highest in Area 1, with significant differences between the areas (df = 2; F = 25.592, p < 0.001) and in pairwise comparisons (p < 0.05 for all pairs). Most *R. mangle* individuals belonged to lower basal area classes (Fig. 4). The height of *R. mangle* individuals also differed significantly between the three areas (df = 2; F = 20.134, p < 0.001), with Area 1 having significantly taller trees compared to the other two areas (p < 0.001 for pairs A1:A2 and A1:A3) (Table 2). The distribution of *R. mangle* individuals in height classes did not show a consistent pattern between the areas (Fig. 5).

Seedlings

Laguncularia racemosa was the most dominant species in the seedling layer, with the highest abundance and relative dominance, followed by *R. mangle* and *A. schaueriana* sequentially. The differences in abundance were statistically significant (df = 2,

$F=6.934$, $p=0.001$), and *A. schaueriana* differed significantly only from *L. racemosa* in pairwise comparison ($p=0.001$). Seedlings of *R. mangle* were the tallest, while *L. racemosa* seedlings were the shortest. Once again, these differences were statistically significant ($df=2$; $f=479.992$; $p<0.001$), with pairwise comparisons showing significant height differences ($p<0.01$ for all pairs) (Table 3).

Avicennia schaueriana

Seedling abundance and relative density were highest in Area 1, with the lowest values recorded in Area 2. However, there were no statistically significant differences in abundance between the three areas ($p=0.073$). This species seedlings were the tallest in Area 2, but there were no significant differences between the areas ($p=0.410$) (Table 3; Fig. 6).

Laguncularia racemosa

Seedling abundance and relative density were highest in Area 1 and lowest in Area 2. Also, there were no significant differences detected in seedling abundance ($p=0.855$). In terms of height, Area 1 again had the tallest seedlings, with significant differences between the three areas ($df=2$; $F=11.261$, $p<0.001$). Area 1 differed significantly from both Area 2 ($p<0.001$) and Area 3 ($p=0.015$) (Table 3; Fig. 6).

Rhizophora mangle

The seedling abundance was highest in Area 1 and lowest in Area 3, with observed significant differences between the areas ($df=2$; $F=6.320$, $p=0.003$) and between Areas 1 and 3 in pairwise comparison ($p=0.02$). Average seedling height did not differ significantly between the areas ($p=0.064$) (Table 3; Fig. 6).

Genetic diversity analysis

In this study, SNPs were analyzed from remnant autochthonous plants (REM), allochthonous plants from the beginning of the restoration (PL), later planted adult tress (Pl), and naturally regenerating seedlings (Sl) of the *A. schaueriana* and *L. racemosa* species. The MIG-seq analysis provided 40 polymorphic loci in *A. schaueriana* and 138 in *L. racemosa*.

For *A. schaueriana*, similar values of expected heterozygosity and observed heterozygosity were observed, with no significant difference ($p=0.637$). Seedlings exhibited the lowest observed heterozygosity, while remnant trees had the highest (Table 4). Regarding *L. racemosa*, the expected and observed heterozygosity values were significantly different ($p<0.001$; Table 4), indicating a loss of genetic diversity, likely due to genetic drift. This trend was consistent across all the groups analyzed in the PNMBM, including remnant trees, suggesting a potential long-term reduction in genetic diversity within the PNMBM.

Table 3 Species and area-specific population structure of seedlings in the PNMBM restoration project, including abundance (n, number of individuals), relative density (DeR, percentage), and height (H, cm with standard deviation)

Espécies	Área	*n*	DeR (%)	H (cm)
Av	1	19^{a}	86.4	28.8 ± 14.4^{a}
	2	1^{a}	4.5	35.0^{a}
	3	2^{a}	9.1	15.5 ± 9.2^{a}
	Total	22^{A}	1.5	28.0 ± 14.5^{A}
Lg	1	351^{a}	37.6	18.4 ± 22.3^{a}
	2	260^{a}	27.9	12.6 ± 6.4^{b}
	3	322^{a}	34.5	15.2 ± 8.9^{b}
	Total	933^{B}	62.2	15.8 ± 15.3^{B}
Rh	1	308^{a}	56.6	42.9 ± 16.3^{a}
	2	183^{ab}	33.6	39.7 ± 16.2^{a}
	3	53^{b}	9.7	39.1 ± 11.3^{a}
	Total	544^{AB}	36.3	43.1 ± 18.5^{C}

Av Avicennia schaueriana, *Lg Laguncularia racemosa*, *Rh Rhizophora mangle*

Lowercase letters represent differences in populations of each species when areas are compared, while uppercase letters represent differences between species

Given the limited genetic variation within the PNMBM, the genetic structure was evaluated by multivariate DAPC analysis, which maximizes variation between groups and minimizes variation within groups (Fig. 7). Both species exhibited an overlap in the genetic variance of planted trees (Pl) and seedlings (Sl), suggesting limited propagule dispersion and possibly some inbreeding. The REM and PL individuals were more spread in the DAPC than the other groups, for both species. The Analysis of Molecular Variance (AMOVA) did not detect genetic differentiation between the groups for both *A. schaueriana* ($phiST = -0.066$; $p=0.3427$) and *L. racemosa* ($phiST = -0.0625$; $p=0.4286$), indicating the absence of genetic structure in the restored mangrove within the PNMBM.

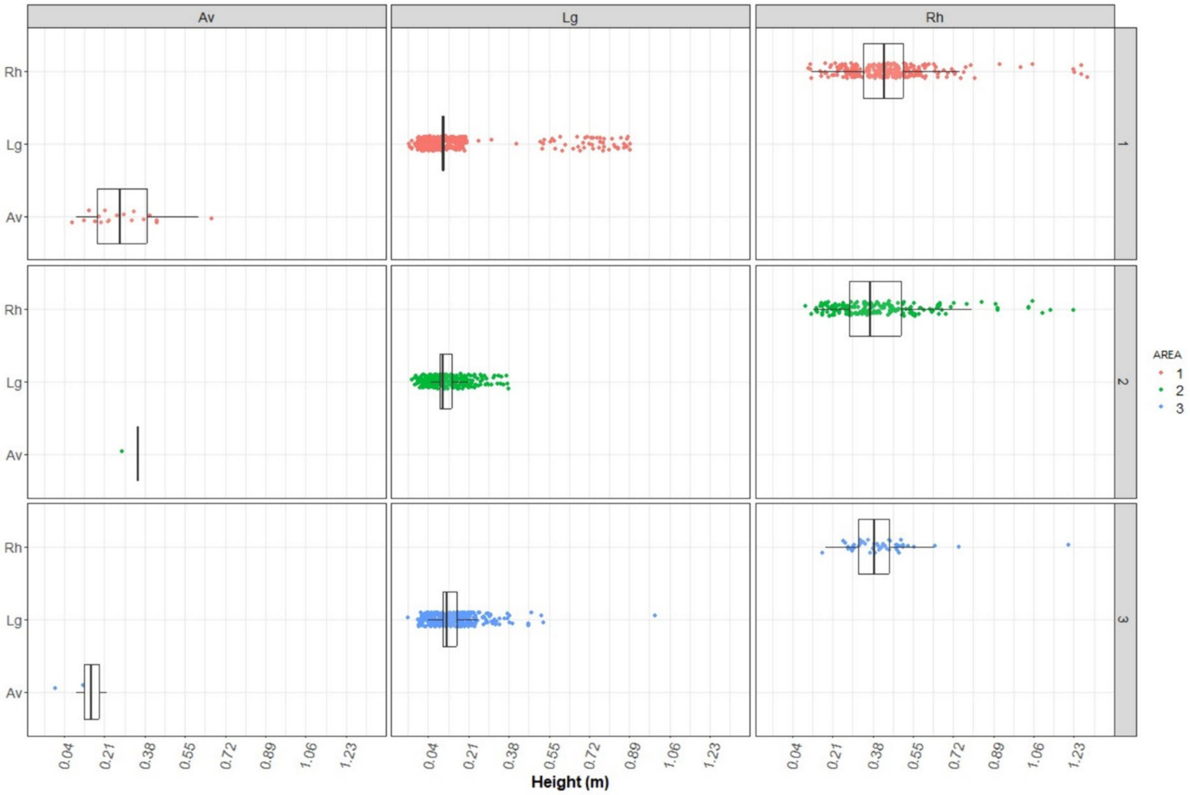


Fig. 6 Boxplot of seedling height values (m) for the three species (vertical grids) in Areas 1, 2, and 3 (red, green and blue, respectively; horizontal grids). Av *Avicennia schaueriana*, Lg *Laguncularia racemosa*, Rh *Rhizophora mangle*

Table 4 Genetic diversity indices of mangrove individuals of *Avicennia schaueriana* and *Laguncularia racemosa* in the PNMBM

	A. schaueriana			L. racemosa		
Group sample	N	He	Ho	N	He	Ho
Rem	8	0.164	0.159	8	0.202	0.121
PL	8	0.150	0.143	8	0.168	0.103
Pl	23	0.186	0.156	24	0.194	0.117
Sl	23	0.169	0.140	23	0.209	0.105
Total/Overall	**62**	**0.180**	**0.148^{NS}**	**63**	**0.208**	**0.112^{***}**

N number of samples, *he* expected heterozygosity, *Ho* observed heterozygosity, *rem* remnant autochthonous plants, *PL* allochthonous plants, *Pl* planted adults, *Sl* seedlings, *NS* non-significant

***p-value < 0.001

Discussion

The United Nations Decade on Ecosystem Restoration (2021–2030) has led to an increase in wetland and mangrove restoration projects. However, there are still significant knowledge gaps regarding restoration methodologies, long-term monitoring, success indicators for mangroves and other wetland ecosystems, and consistent funding sources (Cadier et al. 2020; Waltham et al. 2020). Multidisciplinary

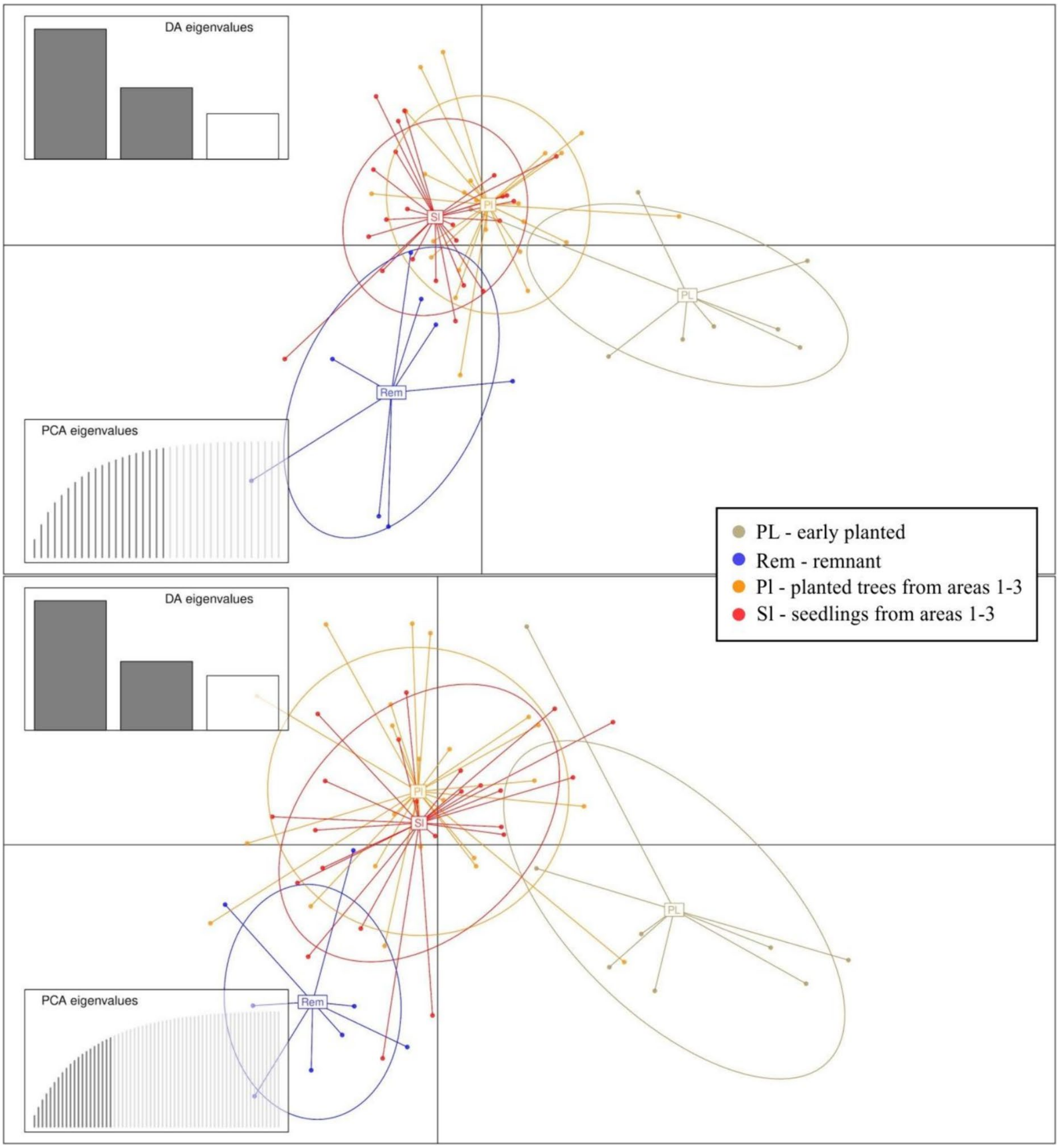


Fig. 7 Discriminant Analysis of Principal Components (DAPC) of mangrove individuals in PNMBM. **Upper graph** *Avicennia schaueriana* groups; **Bottom graph** *Laguncularia racemosa* groups: Remnant autochthonous plants (REM), allochthonous plants from the beginning of the restoration (PL), later planted adult tress (Pl), and naturally regenerating seedlings (Sl)

assessments using innovative and cost-effective techniques for long-term monitoring can help address these critical areas within restoration research.

Vegetation cover obtained with NDVI

Restoration efforts should extend beyond planting to include robust monitoring. This data-driven approach informs post-planting management decisions, ultimately ensuring successful mangrove re-establishment (Bunting et al. 2018; Zhang et al. 2021; Liu et al. 2022; Fan et al. 2023). NDVI effectively captures vegetation health changes at both spatial and temporal scales (Kalisa et al. 2019). The results shown here suggest overall restoration success in the PNMBM, especially after turning it into a protected area in 2012. However, complementing this with phytosociological analysis provides a more nuanced perspective. While NDVI indicated positive trends, the phytosociological data revealed a complex pattern. Older restored areas exhibited characteristics of an intermediate-stage mangrove forest (Bosire et al. 2008; Salmo et al. 2013). Planting success was predominantly driven by *L. racemosa*, the dominant species in the PNMBM, with *R. mangle* occupying specific niches and *A. schaueriana* facing establishment challenges.

These findings underscore the limitations of relying solely on coverage indicators like NDVI to evaluate restoration efficacy (Fan et al. 2023). While quantitative measures are valuable (Sahraei et al. 2023; Wang et al. 2023; Sunkur et al. 2024), incorporating qualitative indicators is essential for a comprehensive assessment. The integration of both qualitative and quantitative remote sensing data holds significant potential (Fan et al. 2023; Rondon et al. 2023). Nevertheless, field assessments remain crucial for validating these findings.

Forest structure 20 years after planting trees

The three restored areas showed different structural characteristics, reflecting the time since their restoration. Area 1 was restored approximately 20 years ago and had a lower abundance and relative density of individuals compared to Areas 2 and 3, which were restored roughly 10 years ago. However, individuals in Area 1 were larger and more dominant, indicating an intermediate to advanced successional stage for mangrove ecosystems (Salmo et al. 2013). Conversely, Areas 2 and 3 had a greater abundance (4–5 times higher than Area 1) of smaller individuals, in line with observations from other young mangrove restoration projects (Bosire et al. 2008; Salmo et al. 2013).

While classified as an intermediate to advanced successional stage, the structural attributes of Area 1 are not as developed as those found in natural or passively restored mangrove forests. Typically, natural or passively restored areas can have double the basal area measured in this study (Berger et al. 2006; O'Connor et al. 2020). Various studies have shown that this trend is common in restored mangrove areas. The extent of former deforestation and the severity of impacts on the mangrove before restoration can affect the outcomes (Martinuzzi et al. 2009; Hanggara et al. 2021). Additionally, restoration practices such as seedling spacing, size, and subsequent management play a significant role (Lewis III 2005; Sukardjo et al. 2014; Sasmito et al. 2019). At the same time, factors such as flood frequency, salinity, nutrient input, exposure to light and wave action, and the dynamics of formation and recolonization of natural vegetation gaps affect the speed of growth and establishment of species (i.e., Duke et al. 2007).

Restoration dynamics affect the forthcoming forest structure

The analysis of the three planted species revealed differences in their population structures within the PNMBM. *Laguncularia racemosa* and *R. mangle* exhibited denser populations with greater basal area and dominance. In contrast, *A. schaueriana* had taller individuals. This pattern can be explained by established efficiency, with greater development and lower mortality rates after planting. Indeed, *A. schaueriana* suffered more significant losses during its establishment (A. Silva, personal communication). Possibly, the environmental conditions of the area, such as high temperatures and salinity, may have limited the establishment and survival of *A. schaueriana* propagules in the initial stages of development, as the species has specific ecophysiological requirements in this initial phase of development (Twilley and Day Jr 2012).

The forest structure of PNMBM featured *R. mangle* as the second most dense species. This species is considered dominant in Brazilian mangroves, typically found in areas with organic matter and low salinity, such as fringes and muddy sediments (Schaeffer-Novelli et al. 1990; Cintrón-Molero et al. 2023). However, lower seedling densities of *R. mangle* were observed due to high propagule mortality rates in the greenhouses and seedling predation by crabs in the field (A. Silva, personal communication). Crab predation is a significant factor influencing the distribution and density of mangrove species (e.g., Lima 2018), potentially affecting population regeneration dynamics (Fruehauf 2005), especially in restored areas.

Natural regeneration after restoration

Some studies suggest that the natural growth of new seedlings in restored mangroves may take up to 15 years (Proffitt and Devlin 2005), indicating that the age of restoration is critical for natural regeneration (Bosire et al. 2008). However, the restored areas of the PNMBM showed high densities of seedlings. Notably, Area 1, which was restored 20 years ago, had the highest number, density, and height of new seedlings. Despite facing challenging and slow restoration due to unfavorable environmental conditions for seedling growth, the studied area displayed strong regrowth. It is important to note that the characteristics of the mangrove substrate change progressively with restoration (Salmo et al. 2013). Thus, the aging and maturing of the planting sites likely play a crucial role in soil rehabilitation and seedling establishment (i.e., Osland et al. 2012). Possibly, Areas 2 and 3 benefited from improved substrate conditions established in Area 1, maybe through material transport by tides, which facilitated faster seedling establishment in these younger areas (Elster 2000; Lewis et al. III 2019).

The structural attributes of *L. racemosa* seedlings were the highest among the three species studied. This is consistent with its role as a pioneer species, capable of colonizing forest gaps, disturbed areas, and newly created bare habitats, possibly forming monodominant stands (Tomlinson 1986; Coelho Jr. 1998; Fromard et al. 1998; Twilley and Day Jr 2012; Nevill et al. 2016). The *L. racemosa* species has ecological plasticity, allowing it to tolerate wide variations in salinity (Jiménez and Soto 1985) and light availability (Rodriguez-Rodriguez et al. 2018). These characteristics enable its propagules to be deposited in these areas, where they can germinate quickly and establish dense seedling banks (Schaeffer-Novelli and Cintron-Molero 1986; Soares et al. 2017).

Recruitment of *R. mangle* is usually expected to reflect the forest structure, with higher recruitment rates and seedling densities in areas where it dominates the arboreal stratum (Proffitt et al. 2006; Lima et al. 2024). However, the highest seedling abundance for this species was observed in Area 1, which was dominated by *L. racemosa* adult trees. This could be attributed to the favorable structural characteristics of Area 1, such as a denser canopy that reduces light reaching the ground, a more consolidated substrate, potentially higher nutrient availability (Koch 1997; Lima et al. 2024), lower environmental stress (Krauss et al. 2008; Simpson et al. 2017), and improved hydrodynamic regime (Osland et al. 2012). These factors may contribute to the successful recruitment of *R. mangle* in this particular area.

On the other hand, *A. schaueriana* showed the most limited recruitment across the PNMBM. Although it is recognized as a pioneer species capable of colonizing new and disturbed areas (Costa et al. 2014), there seem to be minimum environmental requirements necessary for propagule germination and seedling establishment (Scholander et al. 1962). Additionally, the limited number of adult *A. schaueriana* suggests insufficient propagule production for effective recolonization. Therefore, our results indicate that *A. schaueriana* populations in the PNMBM will likely require local management through the production and planting of additional seedlings, especially in areas with denser canopies exceeding 30% light penetration (Silva and Maia 2019). Management strategies to mitigate crab predation should also be considered.

Genetic diversity monitoring

Heterozygosity, as established by Nei (1973), is widely used to assess genetic diversity in natural populations and species. The difference between observed and expected heterozygosity values indicates deviations from Hardy-Weinberg equilibrium, reflecting the influence of genetic drift, limited gene flow, small populations, inbreeding, and other evolutionary processes (Frankham et al. 2010). In the PNMBM area, *L. racemosa* showed notably low genetic diversity, as already shown by previous works (Granado et al. 2018). However, the difference between observed and expected heterozygosity is a significant new result from this area. Although these values result from long-term evolutionary processes, restoration may negatively affect local genetic diversity. The methodology employed in PNMBM, which relied on planting saplings derived from local propagules, could have inadvertently fostered inbreeding and exacerbated genetic erosion within the area. On the other hand, *A. schaueriana* showed similar low He and Ho values compared to a previous study using ISSR markers (Granado et al. 2018), also indicating a loss of genetic diversity but no deviation from Hardy-Weinberg equilibrium.

Genetic erosion can have several detrimental consequences, including inbreeding depression (reduced fitness due to mating between closely related individuals) and outbreeding depression (reduced fitness due to mating with highly dissimilar individuals). Over time, these factors can lead to the emergence of deleterious mutations and maladaptation (Leroy et al. 2018). In essence, genetic erosion undermines the fitness of individual organisms and entire populations, rendering them more vulnerable to environmental stresses (Bijlsma and Loeschcke 2012). So, restoration practitioners should take into consideration their potential to negatively impact the genetic diversity of local populations.

Gene flow can counteract genetic erosion

Natural regeneration and gene flow, mediated by pollen and propagule dispersal, can mitigate the negative effects of inbreeding on genetic diversity over successive generations. Fortunately, the PNMBM area is surrounded by nearby mangroves, including the largest conserved mangrove area of Rio de Janeiro state, located in Guanabara Bay. Previous studies have demonstrated higher genetic diversity in this conserved area (Granado et al. 2018), indicating a positive outlook for the future of the *L. racemosa* population in PNMBM. With minimal future pressures, this population may recover genetically through gene flow over multiple generations. However, continuous conservation efforts and management strategies are crucial to mitigate and control existing and emerging threats such as real estate speculation, deforestation, rising sea levels (associated with climate change), and pollution (Ferreira and Lacerda 2016).

Laguncularia racemosa primarily has hermaphroditic flowers and a generalist pollination system, allowing for self-fertilization and self-pollination. However, geitonogamy (pollination between neighboring flowers on the same plant) is favored due to pollinator behavior (Nadia and Machado 2014). This preference for outcrossing and geitonogamy may help lessen the inbreeding effects observed in PNMBM, augmented by the restoration process. Conversely, *A. schaueriana* has a dominant outcrossing reproductive system. While it is self-compatible, it primarily relies on a generalist pollination system with a high dependence on pollinators for fruit formation (Nadia and Machado 2014; Mori et al. 2015a).

Studies have identified the generalist fly *Palpada albifrons* as the predominant visitor to flowers of both *L. racemosa* and *A. schaueriana* (Diniz et al. 2022). This widely distributed fly seems to play a significant role in the reproduction of these mangrove species (Montoya et al. 2012). Although competition among pollinators can limit reproductive efficiency in some plant species, it is not a concern for *L. racemosa* and *A. schaueriana* due to their differing flowering patterns in Brazil (Nadia et al. 2012). However, potential competition for pollinators could arise if co-flowering occurs with other mangrove species like *A. germinans*, which has been observed to outcompete *L. racemosa* (Landry 2013).

The overlap of Pl and Sl samples in the DAPC analysis suggests that most seedlings in the area likely originated from propagules dispersed from nearby mother trees. This limited propagule dispersal from external sources could jeopardize the genetic diversity of future generations within PNMBM. In contrast, *A. germinans* possesses a more efficient seed (propagule) dispersal system than pollen dispersal. And gene flow through seeds is one to two times higher than through pollen, contributing to the maintenance of higher genetic diversity levels in this species (Mori et al. 2015b). This difference in dispersal mechanisms likely explains the observed contrast in genetic diversity between *A. schaueriana* and *L. racemosa*. Additionally, pollution and solid waste accumulation in the PNMBM could significantly hinder the arrival and establishment of propagules, covering the soil, suffocating the germinating seed, and causing heavy metal contamination. Both species rely on hydrochory (water dispersal) for propagule dispersal and require low tide and exposed soil for successful establishment (Tomlinson 1986).

Data-driven restoration practices

Mangrove restoration efforts should extend beyond simply restoring forest structure and biodiversity. These ecosystems play a critical role in carbon sequestration, contributing to mitigating global climate change (Krauss et al. 2014; Sharma et al. 2020). However, studies suggest that restored areas may require up to 17 years to achieve blue carbon stock levels comparable to reference, undisturbed mangroves (O'Connor et al. 2020). This highlights the importance of long-term management and monitoring of restored wetlands.

Effective management practices and monitoring programs should be designed with a holistic perspective, considering not only biomass accumulation but also substrate restructuring, microbial activity, water regime, and the full range of ecosystem services provided by mangroves (Semeniuk 1994; Vovides et al. 2011a, b; Smoak et al. 2013; MacKenzie et al. 2016; Soper et al. 2019).

Genetic monitoring, as part of the conservation genetic approaches, is essential for the long-term persistence of restored populations and areas. Evolutionary forces might be unbalanced, leading to the loss of genetic variation by genetic drift (Frankham et al. 2010). This can be caused especially by small population sizes, and limited gene flow and migration between populations. The failure to consider genetic issues in wild management enhances genetic loss. Conversely, the use of genomic conservation can provide precise estimates of effective population size, demographic history, levels of inbreeding, rates of gene flow, differentiation among populations, and taxonomic status (Frankham 2010).

Combining all the results obtained in this work, we observed two points that need urgent action. First is the very low abundance of *A. schaueriana* adults and seedlings in the restored area. Since there are several remnant trees of this species, we recommend mediated propagule establishment and seedling growth in a controlled area of the PNMBM. For genetic diversity improvement, we recomend human-mediated propagule dispersal. The propagules should be collected from close populations with higher genetic diversity, such as Guapimirim Environmental Protected Area (Granado et al. 2018). Both management actions proposed here have low implementation costs and allow the increase of genetic diversity pool as well as the abundance of mixed trees within PNMBM.

Conclusion

The integration of genetic diversity, phytosociology, and remote sensing analysis provided a comprehensive and detailed view of the success of the restoration project at Barão de Mauá Natural Municipal Park. These complementary methods accurately assessed the ecosystem's conservation and may guide data-driven interventions, ensuring the long-term survival of the restored mangrove forest.

The observed differences in recovery patterns across the three areas, with varying ages since active planting initiation, suggest that exceeding 20 years may be necessary for critical vegetation cover restoration and development. Furthermore, the study identified two mangrove species that require further investigation and management techniques to strengthen the population and increase genetic diversity within the PNMBM. Implementing these management practices is crucial for the establishment of ecologically and genetically viable populations. Without intervention, it would take much more than 20 years and a high number of generations with effective gene flow for these species to achieve a significant increase in genetic diversity naturally.

The area, with the potential to serve as a model for mangrove restoration initiatives worldwide, holds significant promise. As a young mangrove forest, it will continue to undergo successional stages until it matures, potentially improving its genetic diversity naturally. To maintain this process, it is essential that protection measures are maintained and that conservation projects in Guanabara Bay are initiated as quickly as possible. Furthermore, it is crucial that other degraded mangroves are identified and receive restoration iniciatives using the PNMBM experience as a model of successful mangrove restoration. Considering the projections of rising sea levels that could affect approximately 9 million people living in seven municipalities around the Guanabara Bay, restoring, monitoring, and manging mangroves is urgently needed.

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Author contributions Study conception and design were performed by CFL and AFNF. Material preparation and data collection were performed by AAS, GB, CMT, and DT. Data analysis, manuscript writing, and revision were performed by all authors. All authors read and approved the final manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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