

Article

Early Changes in Soil Organic Carbon Following Ecological Restoration in Mangroves Invaded by *Acrostichum aureum*

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Abstract

Mangrove ecosystems store large amounts of soil organic carbon (SOC). However, degradation processes associated with invasive species can alter vegetation structure, hydrological conditions, and carbon cycling, with uncertain consequences for SOC storage and greenhouse gas emissions. This study evaluated changes in SOC stocks to 0–50 cm depth, soil CO₂, CH₄, and N₂O fluxes, and early restoration responses four years after ecological restoration in the Térraba–Sierpe National Wetland, Costa Rica. Comparisons were conducted among a conserved mangrove, a degraded mangrove dominated by *Acrostichum aureum*, and three restored sites subjected to hydrological rehabilitation with contrasting reforestation intensities. The degraded site showed significantly higher SOC contents (171 ± 31 Mg C ha^{−1}; $p < 0.0001$) compared to the conserved site (103 ± 26 Mg C ha^{−1}). CO₂ fluxes did not differ significantly between March and October. CH₄ and N₂O fluxes remained below the detection limits in most measurements. Redundancy analysis identified a significant association between vegetation composition and the measured environmental variables ($p = 0.005$). Higher CO₂ emissions were associated with the dominance of *A. aureum*. Plant density was positively related to SOC content ($R^2 = 0.78$). MR1 site, where hydrological rehabilitation was combined with high-density reforestation, had significantly higher SOC content than the degraded site (242 ± 24.3 Mg C ha^{−1}; $p < 0.001$). Soil CO₂ emissions at MR1 were also significantly lower than at the degraded site ($p = 0.001$). This study provides a pioneering field assessment of mangrove restoration through the control of *A. aureum* invasion. The results suggest that restoration design may influence soil carbon storage during the early stages of recovery.

Keywords: blue carbon; invasion of plants; hydrological rehabilitation; reforestation



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1. Introduction

Mangrove forests are among the most important ecosystems for climate change mitigation because they store large amounts of atmospheric carbon and protect coastal communities from extreme hydrometeorological events [1]. Globally, mangroves are recognized as highly efficient blue carbon ecosystems, with a substantial proportion of their carbon stored in soils, where low-oxygen conditions reduce the mineralization of soil organic matter (SOM) and allow carbon to persist over long periods [2].

However, global mangrove cover declined by more than 500,000 ha between 1996 and 2020 because of multiple anthropogenic and natural pressures [3]. Beyond habitat loss, mangrove degradation is strongly associated with changes in hydrological regime, or hydroperiod, and in the physicochemical quality of pore water and soil [4]. Altered tidal connectivity and freshwater inputs can modify hydrological conditions and, together with eutrophication, contaminant discharge, and climatic variability, shift salinity, redox potential, and oxygen availability in pore water beyond the tolerance limits of dominant mangrove species [4–7]. These changes induce physiological stress, reduce canopy structure and vigor, and alter the soil microbial processes that regulate SOM mineralization; in addition to these, they also weaken ecosystem resilience, increasing vulnerability to further disturbance and posing a risk to mangrove functioning [8,9].

Progressive canopy loss increases light availability and reduces competition for resources, creating conditions that favor the expansion of opportunistic plant species [10]. In mangrove ecosystems, this can increase the likelihood of biological invasion by species adapted to open habitats, particularly where anthropogenic disturbance has reduced canopy cover and facilitated their establishment and spread [11].

The accumulation of SOM is a key ecosystem function for climate change mitigation because it enables carbon storage. However, this reservoir can be altered by anthropogenic changes in vegetation composition and structure [12]. In mangroves, invasion-driven shifts in floristic composition can alter soil microbial communities and rates of organic-residue decomposition, thereby affecting soil CO₂ and CH₄ fluxes [13,14]. These changes can also reduce biodiversity, including macrobenthic communities that play an important role in litter fragmentation and nitrogen and phosphorus release [15], altering nutrient transfer to adjacent ecosystems that sustain coastal fisheries production [16]. Socioeconomic activities such as fisheries and tourism may also be negatively affected through the reduced availability of nursery and feeding habitats for fish, crustaceans, and other commercially important species, whether resident or migratory [17]. In addition, dense stands of some invasive plants may restrict movement of large wild animals [10].

Among the invasive species that frequently colonize disturbed mangroves is the fern *Acrostichum aureum* L. (Pteridaceae). In Central America, *A. aureum* invasion has been documented in several countries, including Colombia, Panama, and Costa Rica [18–20]. In the Térraba–Sierpe National Wetland, Costa Rica, this fern has displaced approximately 1600 ha of mangrove forest [18]. This fern is one of more than 50 plant species reported to exhibit invasive behavior in mangroves worldwide [10]. Of particular concern is that approximately 70% of these species show long-term persistence. Early detection and effective control programs should therefore be incorporated into ecosystem management and conservation strategies [10].

Various strategies have been used to control invasive plants in mangroves, but approaches such as manual removal and agrochemical application often have limited effectiveness because they can promote reinvasion or create risks of environmental contamination [21]. By contrast, effective control requires an understanding of the ecological processes that structure plant communities, including interspecific competition for light, local environmental conditions, and successional dynamics [22]. In this context, ecological restoration

can provide a more effective strategy, particularly when it prioritizes hydrological rehabilitation to restore natural water flow and tidal exchange. Combined with propagule planting, hydrological rehabilitation can promote the recovery of native mangrove vegetation and help re-establish carbon storage [23,24].

Although *A. aureum* is recognized as one of the plant species involved in mangrove invasions in tropical regions, it has received relatively little attention. Existing studies have focused mainly on its physiological and botanical traits [25–27]. Its effects on soil organic carbon (SOC) storage and greenhouse gas fluxes in mangrove ecosystems remain poorly understood, as does the extent to which restoration can reverse invasion-driven changes in ecosystem functioning. The limited available evidence indicates that *A. aureum* has a greater diversity of phenolic compounds and lower leaf decomposition rates than some mangrove tree species [28]. These differences have been linked to changes in carbon accumulation, stabilization, and mineralization processes [23]. In addition, the distribution of *A. aureum* has been associated with areas of higher elevation (microtopography), where topography regulates the frequency of tidal flooding and the salinity of pore water [29]. These topographic variations can modify the hydroperiod and, consequently, the availability of oxygen, microbial activity, the decomposition of organic residues, and the production of greenhouse gases in mangrove soils [30].

We hypothesized that *A. aureum* invasion would be associated with changes in SOC content and soil greenhouse gas fluxes (CO_2 , CH_4 , and N_2O). We also predicted that restored sites would show early signs of recovery, reflected in greater SOC accumulation and greenhouse gas fluxes more like those of the conserved mangrove. We tested these predictions by measuring SOC content, soil greenhouse gas fluxes, pore-water salinity, soil redox potential, and vegetation composition and structure in one conserved mangrove, one degraded mangrove dominated by *A. aureum*, and three restored sites subjected to hydrological rehabilitation with different reforestation densities.

2. Materials and Methods

2.1. Study Area

The Térraba–Sierpe National Wetland (HNTS), on the southern Pacific coast of Costa Rica, contains one of the largest mangrove expanses in Central America (Figure 1). This wetland supports several mangrove species with restricted Neotropical distributions, including *Pelliciera rhizophorae* Planch. & Triana, together with *Rhizophora mangle* L., *Rhizophora racemosa* G. Mey., and the indicated fern *A. aureum* L. Less abundant species include *Laguncularia racemosa* (L.) C.F. Gaertn., *Conocarpus erectus* L., and *Avicennia germinans* (L.) L. [18].

The floristic composition of the HNTS reflects the salinity and flooding gradients characteristic of tropical estuarine systems in the eastern Pacific. The region supports highly productive, structurally developed mangrove forests within a humid tropical climate. Annual precipitation ranges from 2500 to 5000 mm yr^{-1} . The rainy season extends from May to November, followed by a lower-precipitation season from December to April. Mean monthly temperatures vary little throughout the year and remain close to 27 °C [31].

The HNTS has undergone environmental degradation and a reduction in mangrove cover, with an estimated net rate of approximately 40 ha yr^{-1} between 1948 and 2012. This loss has been associated primarily with land-use change and, to a lesser extent, with the displacement of tree species by extensive colonization of *A. aureum* [18]. In 2018, the French Global Environment Facility (FFEM) implemented a pilot ecological restoration project within a six-hectare polygon in the HNTS, located at 8°52'20.44" N, 83°31'47.84" W, with scientific support from the EPOMEX Institute, Universidad Autónoma de Campeche, Mexico. Hydrological rehabilitation was implemented to restore tidal connectivity and the flooding regime.



Figure 1. Location of the study area within the Térraba–Sierpe National Wetland (HNTS), Costa Rica: (A,B) Location of the five study sites (colored dots): a conserved forest (red), a mangrove degraded by the invasion of *Acrostichum aureum* (blue), and three restored sites (other colors). (C) Frontal view of the dominant vegetation at the conserved site. (D–F) Invasion of *A. aureum* at the degraded site. (G) Vegetation established 4 years after reforestation, combined with hydrological rehabilitation at restored site 1 (restored MR1). (H) Vegetation established at restored site 2 (restored MR2), with lower-density reforestation and hydrological rehabilitation. (I) Evidence of reinvasion by *A. aureum* at restored site 3 (restored MR3), four years later, where restoration included only manual removal of the invasive species and hydrological rehabilitation without reforestation.

Hydrological rehabilitation involved excavating an artificial perimeter canal (Figure 1C) and reconnecting the site to the Sierpe River through two natural channels. These channels were manually dredged to restore the hydroperiod and maintain long-term water exchange between the river and the interior of the wetland. The canal network divided the restoration polygon into three units of approximately 2.0 ha each (Figure 1), designated Restored Mangrove 1 (MR1), Restored Mangrove 2 (MR2), and Restored Mangrove 3 (MR3).

During restoration, reproductive fronds and rhizomes of *A. aureum* were removed manually with support from the local community. The fern material was shredded and arranged in mounds 2 m wide and 40 m long. These mounds were temporarily covered with biodegradable black plastic to suppress regrowth. Once the material had reached an advanced stage of decomposition, the plastic was removed and transferred to a collection site authorized by the National System of Conservation Areas (SINAC).

In 2018, contrasting reforestation strategies were implemented using *R. mangle* and *P. rhizophorae*. MR1 was reforested at high density, whereas MR2 received 50% of the planting density used at MR1. MR3 underwent hydrological rehabilitation only, with no active reforestation. These interventions formed part of the pilot restoration project implemented in the HNTS [32].

2.2. Field Sampling Design

The study included five sites (Figure 1B–F):

- (i) A conserved forest (MCO);

- (ii) A degraded site invaded by *A. aureum* (MDEG);
- (iii) A restoration polygon divided into three restoration units, designated MR1, MR2, and MR3.

Vegetation sampling and measurements of water and soil parameters were conducted in 2022, four years after the restoration actions were implemented in 2018. The study followed a post-restoration spatial comparative design, in which restored sites were compared with reference sites representing conserved and degraded conditions.

A preliminary assessment based on satellite imagery and surveys along the Sierpe River identified extensive areas where mangrove forest had been replaced by monospecific stands of *A. aureum*, with a marked reduction in tree cover. These areas were classified as degraded by fern invasion. In contrast, other sites retained an intact canopy, mature trees, and dominance by mangrove tree species, consistent with the reference-ecosystem criteria of the Society for Ecological Restoration (SER). One such site was selected as the conserved reference site. It represented the structural and functional attributes of a healthy mangrove ecosystem, and its selection was supported not only by the field assessment conducted for this study but also by eight years of ecological monitoring undertaken as part of the FFEM mangrove restoration program, which documented the persistence of its conservation condition and ecological attributes over time [32].

Before sampling, transects were established perpendicular to the shoreline to assess internal variation in vegetation structure, including species composition, canopy height, and stand density, following general recommendations for mangrove sampling [33]. This preliminary assessment revealed no clear internal stratification within the sites. The sites were therefore considered relatively homogeneous.

To address the study objectives, three permanent 100 m² square plots were established at each site as spatial sampling subunits within that site. Plots were separated by at least 20 m to reduce local spatial dependence. This spacing also reflected logistical constraints associated with tidal dynamics and travel between sites [33,34].

Each plot was treated as a sampling subunit within its respective site rather than as an independent replicate of the conserved, degraded, or restored condition. This design allowed within-site variability to be characterized. Statistical inference was therefore restricted to comparisons among the sampled sites within the Térraba–Sierpe National Wetland as a case study and cannot be generalized to other mangrove systems. Within this design, sites were the units of ecological comparison, while plots were sampling subunits used to characterize spatial heterogeneity within each site. This approach standardized sampling effort and facilitated comparisons among sites with contrasting vegetation structure, including the restoration site with the higher planting density (MR1).

2.3. Vegetation Structure

At the conserved site, a forest inventory was conducted following standard criteria for the structural characterization of mature mangrove forests [35,36]. All trees with a stem diameter ≥ 5 cm were recorded and identified to species. At the restored sites, all tree individuals within each plot were recorded, regardless of size, to capture the vegetation structure established through restoration. All *A. aureum* individuals present in plots at the degraded and restored sites were also recorded. Total plant density was expressed as individuals per hectare (ind ha⁻¹), and the relative dominance of each species was calculated as a percentage.

Field observations indicated that *A. aureum* exhibited clonal growth, with clusters of fronds emerging from a relatively identifiable rhizomatous base (Figure S1). For sampling purposes, each cluster was treated as an individual to facilitate comparison of vegetation-structure metrics between fern-dominated and tree-dominated sites.

For *Rhizophora* spp., stem diameter was measured 30 cm above the highest prop root using a diameter tape. Tree height was estimated with a Haga altimeter at the conserved site and with a measuring tape at the restored and degraded sites. For *A. aureum*, the height of three fronds per individual was measured in each plot, from the base of the petiole to the apex.

2.4. Pore-Water Parameters

Pore water refers to the liquid fraction retained in soil pores within the mangrove root zone, whose physicochemical characteristics regulate vegetation growth and development [8]. Samples were collected using PVC pipe collectors, or piezometers, installed at a depth of 0–50 cm below the soil surface [37]. At each study site, one piezometer was installed per plot to capture spatial variability in the physicochemical characteristics of pore water within each condition. During monitoring, salinity was measured in practical salinity units (PSUs) using a refractometer (ATAGO, Inc., Bellevue, WA, USA), and redox potential (mV) was measured using a multiparameter probe (HQ11d, Hach, Loveland, CO, USA). Measurements were taken during two sampling campaigns in 2022, in March and October.

2.5. Soil Parameters

Soil organic carbon (SOC) stocks were assessed within the upper 0–50 cm of the soil profile. Three plots were established at each of the five study sites, and one soil core was collected from each plot, yielding a total of 15 cores. Sampling was conducted during the low-precipitation season and at low tide to facilitate core extraction and reduce logistical constraints associated with flooding. Soil cores were collected using a PVC corer 50 cm long and 6.5 cm in internal diameter, fitted with a semi-cylindrical insert to minimize compaction during extraction. Each core was divided into three depth intervals: 0–15, 15–30, and 30–50 cm [38], yielding 45 soil samples for laboratory analysis.

Soil samples were dried in a convection oven at 60 °C to constant weight, thereby minimizing bias caused by differences in moisture content and allowing comparable estimates of carbon stocks [38]. Dry mass was used to calculate soil bulk density (BD). Samples from each depth interval were then homogenized manually, and 10.00 g subsamples were mechanically ground using a TissueLyser II (Qiagen GmbH, Hilden, Germany). This procedure standardized particle size and improved the representativeness of the small soil aliquots used for elemental carbon analysis [23]. After grinding, subsamples were weighed into silver capsules using a XP6 microbalance (Mettler-Toledo International, Inc., Greifensee, Switzerland) with a precision of 1 µg.

Because coastal wetland soils may contain shell fragments and other carbonate materials that contribute to total carbon, samples were treated with hydrochloric acid (HCl) to remove inorganic carbon. This ensured that subsequent analyses quantified soil organic carbon (SOC) only. After HCl treatment, SOC concentration was determined as a percentage by dry combustion using a Flash 2000 elemental analyzer (Thermo Fisher Scientific Inc., Waltham, MA, USA), calibrated with certified reference materials following the analytical method described in [33].

SOC stocks were calculated separately for each depth interval and expressed as megagrams of carbon per hectare (Mg C ha^{-1}), using soil bulk density, carbon concentration, and interval thickness. Values from the three depth intervals were then summed to estimate cumulative SOC stocks to 0–50 cm depth. A detailed description of the calculation procedure and the unit-conversion factors required to express results in Mg C ha^{-1} is provided in [34].

Soil bulk density (BD) was calculated by dividing the dry mass of each sample by its volume, determined from the core diameter and sampling depth. Soil organic matter

(SOM) was quantified as a percentage of dry mass using the loss-on-ignition (LOI) method. Separate, previously ground soil subsamples were combusted in a muffle furnace at 550 °C for 4 h following standard procedures, as described in [39].

2.6. Soil Gas Fluxes

Soil gas fluxes were measured using the static cylindrical chamber method, following a procedure adapted from [40]. Chambers were constructed from PVC tubes measuring 15 cm in diameter and 77 cm in height and were fitted with airtight valves at the top.

Measurements were conducted at each site during two sampling campaigns in 2022: one in March, during the low-precipitation period, and one in October, during the high-precipitation period. In each campaign, two chambers were installed per site and treated as spatial subsamples to characterize within-site variation in gas fluxes, yielding a total of 20 observations. Because the study followed an observational design, comparisons were made among the sampled ecological conditions without inferring causal effects beyond those supported by the study design.

Each chamber was inserted 10 cm into the soil, and the valve was left open for 15 min to allow the internal atmosphere to equilibrate. The valve was then closed, and the chamber air was mixed using a syringe. An initial 20 mL gas sample (C_i) was collected through the valve at the top of the chamber, followed by a final sample (C_f) after a 3 h incubation period.

Samples were analyzed in the laboratory by gas chromatography coupled with mass spectrometry using a TRACE 1310 gas chromatograph and an ISQ QD single-quadrupole mass spectrometer (Thermo Scientific, Waltham, MA, USA). Chromatographic separation was performed using a TRACE GOLD™ GC column (30 m × 0.32 mm internal diameter × 10 µm film thickness; Thermo Fisher Scientific), with ultra-high-purity helium as the carrier gas. Compounds were identified by comparing their mass spectra with entries in the NIST spectral library.

Calibration curves for CH₄, N₂O, and CO₂ were prepared from certified 5000 ppm gas standards (Infra Gases Portable Quark®, Tijuana, Mexico). Serial dilutions were produced using ultra-high-purity helium and Tedlar® bags designed for gas storage and transport. Gas concentrations are expressed in ppm. Samples were injected manually using 1.0 mL precision syringes fitted with Luer–Lock needles and push-button valves (VICI Precision Sampling, Baton Rouge, LA, USA). Gas fluxes were calculated in grams per square meter per day ($\text{g m}^{-2} \text{d}^{-1}$) from the difference between the initial and final concentrations (C_i and C_f), accounting for chamber volume and surface area [40].

2.7. Data Analysis

A dataset was compiled containing all variables measured at the conserved, degraded, MR1, MR2, and MR3 sites. Mean values and standard errors ($\pm$ SEs) were calculated where appropriate for species dominance, plant height and density, pore-water salinity and redox potential, soil organic carbon (SOC), soil organic matter (SOM), soil bulk density (BD), and soil gas fluxes. Normality was assessed using the Shapiro–Wilk test, and homogeneity of variance was evaluated using Levene’s test. Plant density, plant height, salinity, CO₂ fluxes, SOC, SOM, and BD did not initially meet the assumptions of parametric analysis. Box–Cox transformations were therefore applied [41], and the transformed data were reassessed.

One-way analysis of variance (ANOVA) was used to test for differences among sites, with site included as a fixed factor and plot-level observations treated as sampling subunits. Because the sites were unique spatial units and the ecological conditions were not independently replicated, statistical inference was restricted to comparisons among the sampled sites. Results were interpreted cautiously because of the potential for spatial dependence among plots within each site. When ANOVA identified a significant site effect, Fisher’s

least significant difference (LSD) test was used for post hoc comparisons, with significance set at $p < 0.05$.

Plant density, plant height, and redox potential did not meet the assumptions of normality and homogeneity of variance, even after Box–Cox transformation. These variables were therefore analyzed using the Kruskal–Wallis test, followed by Dunn’s post hoc test. Differences in environmental variables between the March and October sampling campaigns were evaluated using t -tests.

Linear regression was used to examine relationships among physical, biochemical, and biological variables, including SOC, SOM, and plant density. Redundancy analysis (RDA) was used to examine associations between vegetation composition and the measured environmental variables, including soil CO₂ fluxes. These analyses were interpreted as exploratory associations within the Térraba–Sierpe National Wetland and were not used to infer causation.

All statistical analyses were performed using Minitab® version 22.1 and XLSTAT Trial version 2026.1.1 (1434), with a significance threshold of $\alpha = 0.05$.

3. Results

3.1. Species Compositions

Plant community composition differed among sites. The conserved site (MCO) was a monospecific stand of *R. mangle*, whereas the degraded site (MDEG) was entirely dominated by *A. aureum*. Among the restored sites, species dominance and vegetation structure varied. *R. mangle* dominated MR1, *P. rhizophorae* dominated MR2, and *A. aureum* dominated MR3.

The conserved site (MCO) had the greatest mean plant height (15.1 ± 0.1 m) and the lowest plant density (416 ± 82.5 ind ha^{−1}) among sites ($H_4 = 12.6$, $p < 0.05$; Table 1). The degraded site (MDEG) showed the opposite pattern, with a lower mean height (2.8 ± 0.1 m) and a significantly higher density ($H_4 = 12.9$, $p < 0.05$). Among the restored sites, MR1 had the highest plant density ($57,779 \pm 2223$ ind ha^{−1}) and a mean height of 2.3 ± 0.2 m. MR2 had the lowest density among restored sites (9444 ± 454 ind ha^{−1}) and a mean height of 2.0 ± 0.1 m. MR3 had intermediate values, with a mean height of 2.7 ± 0.1 m and a density of $22,400 \pm 1386$ ind ha^{−1}. According to Dunn’s post hoc test, plant density did not differ significantly between MDEG and MR3 (Table 1).

Table 1. Species dominance, plant height, and plant density at a conserved site, a degraded site invaded by *Acrostichum aureum*, and three restored sites in the Térraba–Sierpe National Wetland, Costa Rica. Values are presented as mean $\pm$ standard error (SE). Different lowercase letters within the same column indicate significant differences among sites according to Dunn’s post hoc test ($p < 0.05$).

Sites	Height (m)	Density (indha ^{−1})	Species Dominance (%)
Conserved	15.1 ± 0.1 c	416 ± 82.5 d	<i>Rhizophora mangle</i> : 100
Degraded	2.8 ± 0.1 b	$22,500 \pm 1.443$ c	<i>Acrostichum aureum</i> : 100
Restored MR1	2.3 ± 0.2 ab	$57,779 \pm 2.223$ a	<i>Rhizophora mangle</i> : 72 <i>Laguncularia racemosa</i> : 21 <i>Pelliciera rhizophorae</i> : 7
Restored MR2	2.0 ± 0.1 a	9444 ± 454 b	<i>Pelliciera rhizophorae</i> : 68 <i>Rhizophora mangle</i> : 25 <i>Acrostichum aureum</i> : 5 <i>Laguncularia racemosa</i> : 2
Restored MR3	2.7 ± 0.1 b	$22,400 \pm 1386$ c	<i>Acrostichum aureum</i> : 100

3.2. Physicochemical Characteristics of Pore Water

Mean salinity was similar among sites when data from March and October were combined. Salinity was 18.0 ± 4.8 PSU at the conserved site (MCO) and 14.7 ± 1.1 PSU at the degraded site (MDEG), while values at the restored sites ranged from 15.0 to 17.5 PSU (Table 2). No significant differences in salinity were detected among sites ($F = 0.08$, $df = 4$, $p = 0.987$).

Table 2. Salinity and redox potential of pore water at a conserved mangrove site, a site degraded by invasion of *Acrostichum aureum*, and three restored sites in the Térraba–Sierpe National Wetland, Costa Rica. Values are means $\pm$ standard error.

Sites	Salinity (PSU)	Redox Potential (mV)
Conserved	18 ± 4.8	-123 ± 12.8
Degraded	15 ± 1.1	-64 ± 4.3
Restored MR1	18 ± 8.1	-93 ± 41.3
Restored MR2	16 ± 6.6	-124 ± 63.6
Restored MR3	15 ± 6.4	-186 ± 53.3

Mean redox potential varied widely among sites, from -123 ± 12.8 mV at the conserved site to -64 ± 4.3 mV at the degraded site. At the restored sites, values ranged from -93 ± 41.3 to -186 ± 53.3 mV (Table 2). However, these differences were not statistically significant (Kruskal–Wallis test: $H = 8.11$, $df = 4$, $p = 0.087$).

Salinity differed significantly between sampling months ($t = 7.37$, $df = 17$, $p < 0.0001$), with higher values in March and lower values in October (Table S1).

3.3. Characteristics of the Soil

Soil organic matter (SOM) content within the upper 0–50 cm of the soil profile was significantly higher at the degraded site (51%) than at the conserved site (21%; $F = 39.35$, $df = 4$, $p < 0.0001$; Figure 2). Soil bulk density (BD) showed the opposite pattern to SOM (Figure 2). BD was significantly higher at the conserved site (0.53 ± 0.02 g cm^{−3}) than at the degraded site (0.17 ± 0.01 g cm^{−3}). Post hoc comparisons also showed that BD was significantly higher at MR1 than at the degraded site ($F = 21.19$, $df = 4$, $p < 0.0001$; Figure 2).

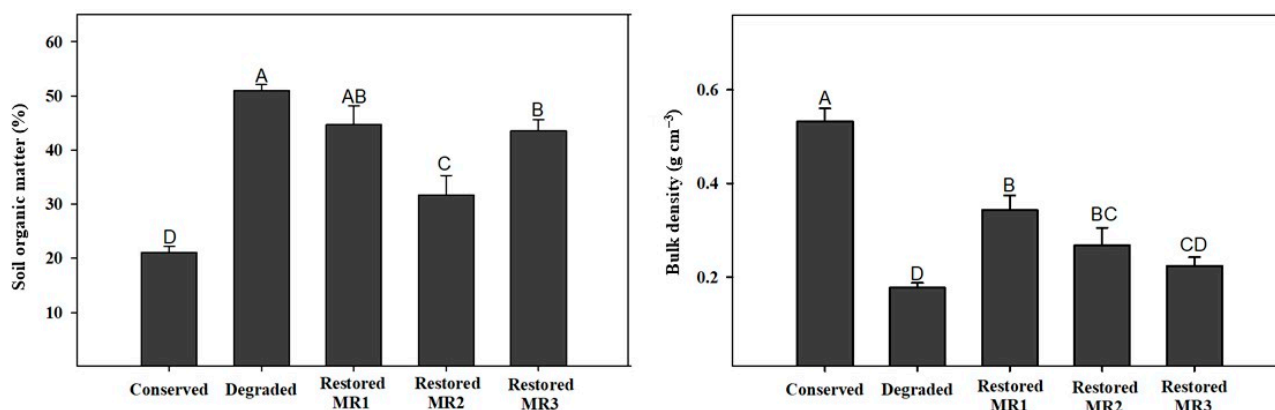


Figure 2. Soil organic matter and soil bulk density at a conserved mangrove site, a site degraded by—*Acrostichum aureum* invasion, and three restored sites (MR1, MR2, and MR3) in the Térraba–Sierpe National Wetland, Costa Rica. Bars represent means and error bars indicate standard errors for samples collected in March 2022. Means that do not share a letter differ significantly at $p < 0.05$.

Soil organic carbon (SOC) stocks also differed significantly among sites ($F = 12.01$, $df = 4$, $p < 0.001$; Figure 3). SOC stocks were 171 ± 31 Mg C ha^{−1} at the degraded site and 103 ± 26 Mg C ha^{−1} at the conserved site. Among the restored sites, MR1 had the highest SOC stock (242 ± 24.3 Mg C ha^{−1}), whereas MR2 and MR3 had values of 126 ± 22.0

and $173 \pm 23.8 \text{ Mg C ha}^{-1}$, respectively. Fisher's post hoc test showed that SOC was significantly higher at MR1 than at MDEG, while MR2 and MR3 did not differ significantly from each other (Figure 3). SOC stocks varied with depth, but the depth-related pattern was not consistent among sites because the site $\times$ depth interaction was not significant (Tables S2 and S3). The lowest depth-specific SOC stock was recorded at 15–30 cm in the conserved site ($30.6 \text{ Mg C ha}^{-1}$), whereas the highest was recorded at 30–50 cm in MR1 ($81.7 \text{ Mg C ha}^{-1}$). Regression analysis showed a positive relationship between SOC content and plant density ($R^2 = 0.78$, Figure 4).

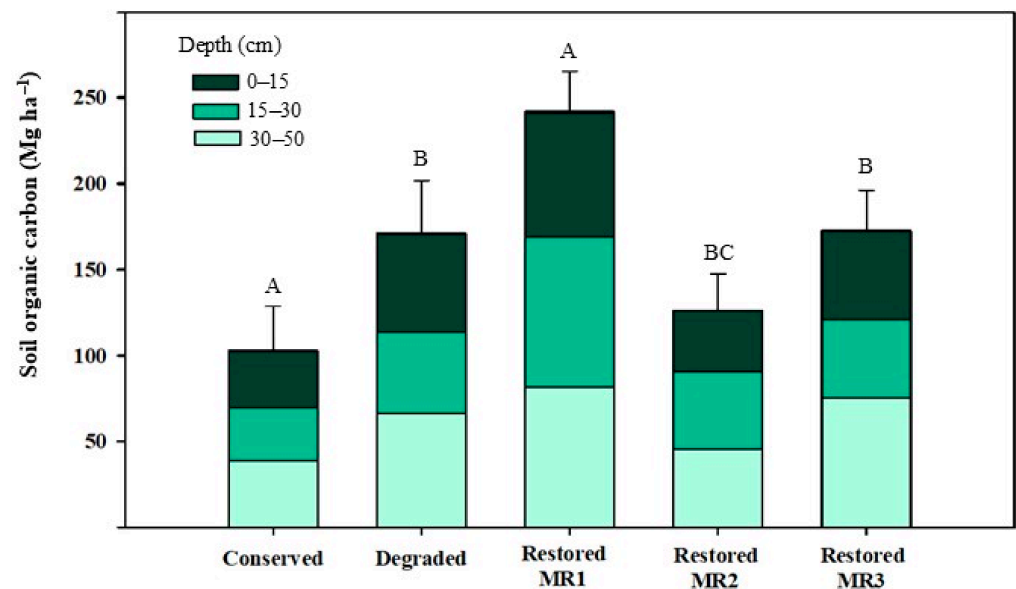


Figure 3. Soil organic carbon (SOC) stocks at a conserved mangrove site, a site degraded by *Acrostichum aureum* invasion, and three restored sites (MR1, MR2, and MR3) in the Térraba–Sierpe National Wetland, Costa Rica. Bars represent mean SOC stocks to 0–50 cm depth based on samples collected in March 2022, and error bars indicate standard errors of the mean. Means that do not share a letter differ significantly at $p < 0.05$.

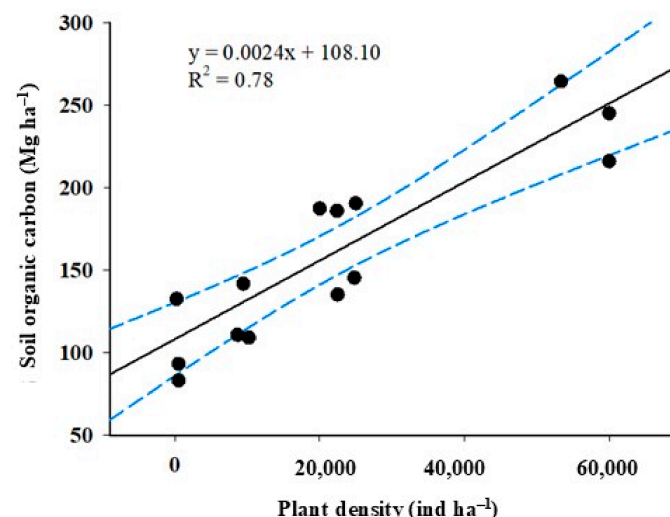


Figure 4. Linear relationship between soil organic carbon (SOC) stocks and plant density across a conserved mangrove site, a site degraded by *Acrostichum aureum* invasion, and three restored sites in the Térraba–Sierpe National Wetland, Costa Rica. Black points represent plot-level values of SOC stocks to 0–50 cm depth and plant density across all sites. The solid black line represents the fitted linear regression, and the shaded area between the blue dashed lines represents the 95% confidence interval.

3.4. Soil Gas Emissions

Averaged across the March and October sampling campaigns, soil CO₂ flux was highest at the degraded site (8.5 ± 1.4 g CO₂ m⁻² d⁻¹) and was significantly greater than at the conserved site (4.7 ± 1.6 g CO₂ m⁻² d⁻¹). At the restored sites, CO₂ fluxes were 1.3 ± 0.91 g CO₂ m⁻² d⁻¹ at MR1, 2.4 ± 0.33 g CO₂ m⁻² d⁻¹ at MR2, and 5.7 ± 1.8 g CO₂ m⁻² d⁻¹ at MR3. CO₂ fluxes differed significantly among sites ($F = 4.8$, $p = 0.011$; Figure 5), but not between March and October ($t = -0.38$, $df = 17$, $p = 0.707$; Table S1).

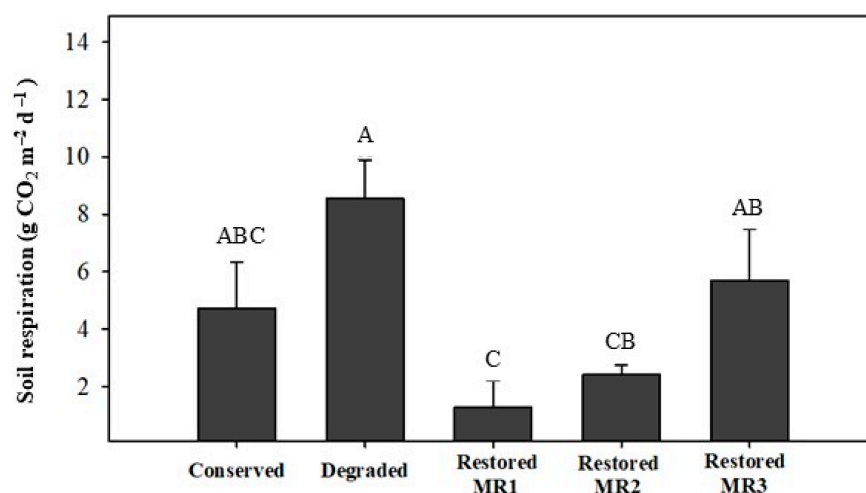


Figure 5. Soil respiration, measured as CO₂ flux, at a conserved mangrove site, a site degraded by *Acrostichum aureum* invasion, and three restored sites (MR1, MR2, and MR3) in the Térraba–Sierpe National Wetland, Costa Rica. Bars represent mean values across measurements conducted in March and October 2022, and error bars indicate standard errors. Means that do not share a letter differ significantly at $p < 0.05$.

Redundancy analysis (RDA) identified significant associations between vegetation composition and the environmental variables evaluated ($F = 0.786$, $p = 0.005$; Table S4). The first two axes together accounted for 99.34% of the explained variation. The RDA biplot indicated that CO₂ fluxes were more closely associated with variation in species composition than with pore-water salinity or redox potential. Specifically, higher CO₂ fluxes were associated with greater dominance of *A. aureum* (Figure S2).

CH₄ and N₂O fluxes were below the detection limit in most plots (Table S1). However, isolated fluxes were detected in individual plots (Table S1). In March, one plot at the degraded site had fluxes of 4.0×10^{-2} g N₂O m⁻² d⁻¹ and 8.0×10^{-3} g CH₄ m⁻² d⁻¹, while one plot at the conserved site had a CH₄ flux of 2.0×10^{-3} g CH₄ m⁻² d⁻¹.

4. Discussion

4.1. Effects of *Acrostichum aureum* Invasion on Mangrove Structure, Soil Organic Carbon, and Gas Emissions

The conserved site in the Térraba–Sierpe National Wetland (HNTS) showed the physiognomic characteristics typical of riverine mangroves, which are recognized as among the most structurally developed mangrove communities [42]. In contrast, the expansion of *A. aureum* was associated with pronounced structural differences within the ecosystem (Figure 1E). The fern now occupies approximately 11% of the HNTS area [18].

Fern density at the degraded site (MDEG) exceeded values reported for other invaded mangroves in Nigeria, where densities of 331–1050 ind. ha⁻¹ have been documented [43]. The complete dominance of *A. aureum* at MDEG (100%) may also restrict the natural

regeneration of mangrove tree species [44]. Together, these findings indicate an advanced stage of invasion in the HNTS and emphasize the need for effective control strategies.

Although *A. aureum* is a natural component of mangrove vegetation, its invasive behavior has been associated with at least two key factors. First, canopy gaps or reduced tree cover increase light availability in the understory. Second, low pore-water salinity may reduce osmotic stress and favor fern growth, allowing it to attain high densities [29].

In this study, *A. aureum* dominance was associated with greater soil carbon storage than that observed at the conserved mangrove site. Similar patterns have been reported for other invasive plants in coastal wetlands [45], although in other cases, invasion has caused substantial declines in this ecosystem service [23].

Recent studies have reported that *A. aureum* leaves contain a greater diversity of phenolic compounds and decompose more slowly than those of some tree species in the Rhizophoraceae [27,28], potentially favoring carbon accumulation. At MDEG, soils also had lower bulk density, higher SOM content, and a porous matrix containing abundant fibrous material throughout the 0–50 cm profile and below this depth (Figure S3). Together, these characteristics are consistent with peat-like organic substrates formed through the progressive accumulation of partially decomposed plant material under conditions of slow decomposition and limited mineral sediment input [46].

The formation of these peat deposits may contribute to the increase in surface elevation observed within *A. aureum*-dominated patches at the same study site [47]. We therefore hypothesize that *A. aureum* may promote the development of an alternative topographic state that facilitates its own establishment by reducing hypoxic stress and indirectly favoring soil carbon accumulation. This interpretation is consistent with previous observations that the species occurs preferentially in relatively elevated areas that are inundated less frequently by tides [29].

However, greater SOM content and lower bulk density associated with peat formation at the degraded site do not necessarily indicate effective long-term carbon storage. Carbon cycling and stabilization depend not only on the quantity of organic matter but also on its quality and its association with mineral particles, factors that are often overlooked [48,49].

In this context, higher SOC stocks did not correspond to an overall improvement in ecosystem functioning within the invaded area. At the site scale, the conserved mangrove dominated by *R. mangle* had lower soil CO₂ fluxes to the atmosphere, whereas the degraded site dominated by *A. aureum* showed the opposite pattern, consistent with the associations identified by the RDA (Figure S2). One possible explanation is the greater surface elevation characteristic of *A. aureum*-dominated stands, as similar topographic changes have been associated with higher CO₂ emissions in Amazonian mangroves [50]. Greater soil elevation may reduce the frequency and duration of tidal inundation and restrict water exchange [51], potentially increasing soil aeration and promoting aerobic decomposition of surface organic matter.

Redox potential also tended to be more positive at the degraded site (Table 2), suggesting relatively more oxygenated conditions, although differences among sites were not statistically significant. These results should therefore be interpreted cautiously because the limited number of sampling campaigns may not adequately capture seasonal and hydrological variability. Higher CO₂ fluxes may also reflect greater root respiration, as reported for opportunistic species with high metabolic rates that support rapid growth [52]. However, soil CO₂ was measured as total flux, without separating autotrophic respiration by roots from heterotrophic respiration by microorganisms. It is therefore not possible to determine which source contributed most strongly to the observed emissions. To determine whether areas invaded by *A. aureum* function as net carbon sinks or sources, future studies should characterize carbon pools and fluxes more comprehensively. This should include

dissolved organic carbon, primary production, carbon burial rates, and separation of the different components of ecosystem respiration [30].

4.2. Restoration Strategies for Fern Control and Their Effects on Soil Organic Carbon and Gas Emissions

Among the restoration strategies evaluated, the interventions implemented at MR1 and MR2 were most effective in controlling *A. aureum*. A plausible mechanism is the progressive closure of the tree canopy following reforestation, which reduces light and space availability in the understory and limits fern establishment and recolonization at high densities. This interpretation may be consistent with previous studies showing that reforestation can contribute to the control of invasive species in mangroves [22,53].

Additionally, the results suggest that the strategies implemented at MR1 and MR2 can support the recovery of mangrove cover. This was reflected in the establishment of *R. mangle* (Figure 1G) and *P. rhizophorae* (Figure 1H), with individuals reaching up to 2 m in height, consistent with successful early-stage recovery over the short term [24,54]. The high regional precipitation may further promote growth and reduce mortality in reforested areas within the HNTS [47], thereby supporting biomass production and photosynthetic activity [55]. Higher plant density may also enhance sediment deposition by reducing water-flow energy during inundation [56]. Such processes can contribute to SOC stabilization through the formation of organo-mineral associations, particularly with Fe and Al oxides and hydroxides [57]. This mechanism may be especially important during the early stages of mangrove restoration, when recently incorporated and relatively labile organic matter predominates [58].

Hydrological rehabilitation through the reconnection of obstructed natural channels and the construction of artificial canals may also contribute to SOC recovery by altering site hydrology and reducing soil respiration. This mechanism may be particularly relevant at MR1, where the lowest CO₂ fluxes were recorded. Increased inundation can reduce soil respiration by restricting CO₂ diffusion to the atmosphere, limiting aerobic decomposition, and suppressing microbial activity under prolonged water saturation and hypoxic conditions [59]. This interpretation is consistent with the lower mean redox potential observed at the restored sites than at the *A. aureum*-dominated degraded site (MDEG).

From a restoration perspective, these findings suggest that the potential contribution of hydrological rehabilitation warrants further evaluation in restoration programs where the hydroperiod has been altered, particularly in fern-invaded areas that may be associated with higher CO₂ fluxes than conserved mangrove sites.

In addition to CO₂, CH₄ and N₂O fluxes were detected, although only sporadically or below the detection limit at most study sites (Table S1). Mangroves are generally reported to exhibit low CH₄ and N₂O emissions, although these fluxes can vary according to conservation status, anthropogenic disturbance, and nutrient availability [60]. The low CH₄ emissions observed in this study may be related to the high sulfate availability associated with marine influence, which has been reported to improve sulfate-reducing microorganisms that suppress methane production [61]. Likewise, the low N₂O emissions may be associated with the reducing conditions typical of flooded mangrove sediments, which have been shown to favor complete denitrification to N₂ and thereby limit N₂O accumulation [62].

5. Conclusions

The invasion of *A. aureum* in the Térraba–Sierpe National Wetland was associated with marked changes in vegetation structure and soil properties, including greater SOC

stocks. However, this increase did not necessarily indicate improved ecosystem functioning because the invaded site also showed higher soil CO₂ fluxes.

Among the sites evaluated, restoration strategies combining hydrological rehabilitation with active reforestation were associated with more effective early control of *A. aureum* and greater recovery of tree cover than hydrological rehabilitation combined with manual fern removal alone. In particular, the reforestation site with the highest planting density (MR1) had the greatest SOC stocks and the lowest CO₂ fluxes, representing an observed pattern consistent with early-stage ecological recovery. Medium- and long-term monitoring is needed to determine whether control of *A. aureum* remains stable and whether the observed changes in SOC stocks and gas fluxes persist over time.

These findings highlight the importance of integrated restoration strategies that consider the physical, physicochemical, biochemical, and biological processes regulating ecosystem functioning. Within the context of this case study, the observed patterns were based on a limited number of measurements per site, and more intensive temporal monitoring is required to strengthen inferences about carbon dynamics. Despite this limitation, SOC stocks, soil CO₂ fluxes, vegetation structure, and related environmental variables may serve as useful indicators for assessing early ecosystem functional recovery and should be incorporated into the funding, design, implementation, and long-term monitoring of mangrove restoration programs.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d18070427/s1>, Figure S1. Field observation of the clonal growth pattern of *Acrostichum aureum*. The red circle indicates a cluster of fronds emerging from a relatively distinct rhizomatous base. Figure S2. Redundancy analysis (RDA) biplot showing the dominance of four mangrove plant species (*Acrostichum aureum*, *Pelliciera rhizophorae*, *Rhizophora mangle*, and *Laguncularia racemosa*) in relation to total plant density, soil respiration (g CO₂ m⁻² d⁻¹), redox potential, and pore-water salinity. The first two axes (F1 and F2) explained 99.34% of the model variance. Figure S3. Soil profile at the degraded site invaded by *Acrostichum aureum* in the Térraba–Sierpe National Wetland, Costa Rica. Table S1. Mean values (±standard error) of pore-water salinity and redox potential and soil CH₄, CO₂, and N₂O fluxes at conserved, degraded, and restored mangrove sites in the Térraba–Sierpe National Wetland, Costa Rica, during March and October 2022. Table S2. Two-way ANOVA of soil organic carbon (SOC) stocks across five mangrove sites representing conserved, degraded, and restored conditions and among soil-depth intervals. The sites comprised one conserved mangrove, one mangrove degraded by *A. aureum* invasion, and three sites subjected to different restoration strategies. NS = not significant; S = significant. Table S3. Soil organic carbon (SOC) stocks at different depth intervals across five mangrove sites representing conserved, degraded, and restored conditions in the Térraba–Sierpe National Wetland, Costa Rica. SE = standard error. Table S4. Results of the RDA relating the dominance of four mangrove plant species (*A. aureum*, *P. rhizophorae*, *R. mangle*, and *L. racemosa*) to total plant density, soil respiration (g CO₂ m⁻² d⁻¹), redox potential, and pore-water salinity. The first two axes (F1 and F2) explained 84.9% of the model variance. Data were collected in March and October 2022.

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