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Conversion of Mangroves Into Rice Cultivation Alters Functional Soil Microbial Community in Sub-Humid Tropical Paddy Soil

Upendra Kumar, Megha Kaviraj, P. Panneerselvam and A. K. Nayak*

ICAR-National Rice Research Institute, Cuttack, India

Conversion of mangrove vegetation into rice cultivation is considerably enhanced nowadays which adversely affects ecological sustainability. Soil microbial community is one of the key indicators to monitor soil health in mangroves. Studies on the variations in the microbial community within mangroves are plenty, whereas reports in mangrove-converted paddy soils are scarce. Therefore, Biolog® eco-plate-based technique was used in this study to assess soil microbial community in the Bhitarkanika (MB) and Sundarban (MS) sub-humid tropical mangroves-converted paddy soil. The results showed that significantly lower soil microbial biomass carbon and enzyme activities were recorded in MB and MS compared to the NRRI (National Rice Research Institute) paddy soil where continuous rice cultivation is being practiced conventionally since 1946 under the sub-humid tropical region. Biolog®-based average well color development (AWCD) was found significantly lower in MS and MB compared to NRRI. Shannon–Weaver and McIntosh indices followed the similar trends of AWCD. A biplot analysis indicated the positive correlation of pH, available phosphorus, actinomycetes population, and phenolic compound utilization under MS, whereas EC and phosphate-solubilizing bacteria were positively correlated under MB. Compared to MS and MB, NRRI paddy soil harbored more carbohydrate-utilizing microbes and showed a positive correlation with fluorescin-diacetate, dehydrogenase, and acid phosphatase. Overall, the present study suggested that the conversion of the Sundarban and Bhitarkanika mangroves into rice cultivation adversely affected the microbial diversity, thereby altering natural sustainability.

Keywords: mangrove, biolog ECO plates®, microbial community, soil enzymes, rice

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****Correspondence:***
Upendra Kumar
ukumarmb@gmail.com
orcid.org/0000-0002-9246-3920

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INTRODUCTION

Mangrove ecosystems constitute a very rich biodiversity of microorganisms which play vital roles in nutrient cycling and regulating the physico-chemical equilibrium in these environments (Alongi et al., 1993; Holguin et al., 1999; Borrell et al., 2016; Atwood et al., 2017). Organic carbon (C) stocks of mangrove ecosystems are measured to have equal or higher than terrestrial tropical forests (Mcleod et al., 2011) and are considered as one of the most important C-sinks in the biosphere (Twilley et al., 1992; Chmura et al., 2003; Nellemann and Corcoran, 2009; and Donato et al., 2011). Besides the natural reservoir of C stocks, the mangrove ecosystem also houses a diverse group of beneficial microbial communities (Holguin et al., 2001; Maria and Sridhar, 2002; and Thatoi et al., 2013). The major microbial community harbored in Indian mangroves is marine algae (60.1%), fungi (11.2%),

and bacteria (7.5%) (Sahu et al., 2015). However, these reservoirs are being lost due to several factors that despoiled the mangrove ecosystem around the world. In recent estimates, nearly 0.1 million ha of the world's mangrove forests was lost from 2001 to 2012 at the rate of 0.7–7% annually, which was around four times higher than that of rainforests (Strong and Minnemeyer, 2015; Thomas et al., 2017). India covers around 7% of the world's mangroves (Kathiresan 2000; Banerjee et al., 2012a) which is being lost at the rate of 2.8% since the last century (Kumar, 2000; Sahu et al., 2015). It is mostly due to the conversion of mangrove forests into agriculture practices (rice cultivation), aquaculture (shrimp farming), and several anthropogenic activities such as intense boating and fishing, dredging, tourism, and port activities (Duarte et al., 2004; Bouillon et al., 2008; Duarte et al., 2010; Kennedy et al., 2010; United Nations Framework on Climate Change, 2012).

Past reports mainly emphasized the microbial communities under the mangrove ecosystem worldwide (Maria and Sridhar, 2002; Thatoi et al., 2013), however, reports related to the functional diversity of the microbial community under mangrove-converted paddy soil are limited. A paddy cultivated soil ecosystem represents one of the best-studied models for soil microbial ecology (Kumar et al., 2020a; Kumar et al., 2021). Rice can be grown in a wide range of soil, climatic, and hydrological conditions including mangrove ecosystems (Bouillion et al., 2008; Kennedy et al., 2010). Variations of the microbial community under paddy soil are drastically influenced by the application of fertilizers (Kumar et al., 2017; Kumar et al., 2018) and pesticides and have tremendous effects on the nutrient dynamics in the soil. For quantification of microbial community and diversity, researchers are currently using many methods under diverse ecosystems including the rice rhizosphere (Kumar et al., 2018; Manjunath et al., 2018). Among these methods, Biolog® eco-microplates are commonly used to assess the functional diversity of soil microbial communities under different ecosystems including rice (Zak et al., 1994; Li S. et al., 2013; Kumar et al., 2017; Pradhan et al., 2019; Kumar et al., 2020b).

Bhitarkanika and Sundarban are two sub-humid tropical mangroves situated in eastern India and have huge reservoirs of the microbial community (Thatoi et al., 2013; Dutta et al., 2015; Arya and Syriac, 2018). Reports indicated that the mangrove forest area of the Bhitarkanika (Chauhan et al., 2017) and Sundarban (Ramesh et al., 2019) have been significantly converted into agricultural land (~50 and ~6% of total area of Bhitarkanika and Sundarban mangroves, respectively) over the last few decades, which is a threat to environmental sustainability with more C-emissions such as methane, thereby reducing the cost-effectiveness of the same land (Priyadarshini, 2015; Chauhan et al., 2017). Moreover, the reclaimed mangroves, including Sundarban, are highly populated and have fallen victim to various adverse effects of climate change and also impacting the salinity regime (Chowdhury et al., 2021a) which might affect the microbial community of that region (Chambers et al., 2016).

Numerous studies indicated the alteration of soil microbial community in Bhitarkanika (Thatoi et al., 2013; Dangar et al., 2016; Behera et al., 2019) and Sundarban (Banerjee et al., 2012b; Das et al., 2012; Bhattacharyya et al., 2019), however, reports on alteration of the microbial community under mangrove-converted paddy soils are limited (Tripathi et al., 2016). Hence, an attempt was made to analyze the significant changes in functional microbial diversity using Biolog® eco-micro plates, chemical, and enzymatic properties of soils of the mangrove-converted paddy soil and compared with NRRI paddy soil where paddy cultivation is being practiced conventionally since 1946. We hypothesized that the conversion of sub-humid tropical mangrove vegetation into rice cultivation may alter its soil microbial community.

MATERIALS AND METHODS

Soil Sampling and Chemical Analyses

Rhizosphere soil (panicle initiation stage of rice crop) samples were collected from two sub-humid tropical mangrove-converted paddy soils from Bakkhali, Sundarban (MS), West Bengal (21° 33′ N, 88° 15′ E) and Dangamal, Bhitarkanika (MB), Odisha (20° 75′ N 86° 85′ E), and ICAR-National Rice Research Institute (NRRI), Cuttack, India (20° 25′ N, 85° 55′ E). A composite sample was made after collecting five soil samples from each location. A portion of the composite soil was air-dried, powdered, and passed through a sieve of 2 mm. This sample was used to analyze the soil pH, electrical conductivity, organic carbon (SOC), and total nitrogen (TN) using an elemental analyzer (Flash 2000; Thermo Scientific), available-P (Bray and Kurtz 1945), and available-K (Piper and CS, 1966) as per standard protocols. The remaining composite soil sample was stored in a refrigerator at 4°C for biochemical analysis. Microbial biomass C was estimated by using chloroform fumigation extraction methods adopted from Vance et al. (1987). The soil enzyme parameters *viz.*, dehydrogenase (DHA), acid phosphatase (ACP), alkaline phosphatase (ALP), and urease were determined using methods referred by Acosta-Martinez and Tabatabai (2000) and Kumar et al. (2018).

Determination of Different Groups of Soil Microbial Population

10 g of soil was suspended in 0.85% sterile saline distilled water (90 ml) and dilutions were prepared from 10^{-2} to 10^{-6} levels. A suitable sterile medium was prepared for each particular group as per the methods referred by Burnett et al. (1957). By using the spread plate technique, 100 µl of soil supernatants were spread uniformly on Petri plates in triplicates and the plates were incubated for 3–7 days at 30 ± 0.1°C and the appeared colonies were counted as colony-forming unit (CFU) g^{-1} soil (Kumar et al., 2017).

For the determination of heterotrophic aerobic bacterial population (HAB), a nutrient agar medium was prepared and diluted suspensions on plates were spread plated and kept for incubation for 4 days at 30°C. The colonies (bacterial) were counted and recorded as CFU g^{-1} soil. Similarly, for the enumeration of fungi and actinomycetes, the same process was carried out in Rose Bengal and actinomycetes isolation agar medium, respectively (Kutzner and Buchenauer, 1986).

TABLE 1 | Physico-chemical properties of soils from conventional and mangrove-converted rice area.

	Conventional paddy soil	Mangrove-converted paddy soils	
Study area	NRRI (±SD)	MS (±SD)	MB (±SD)
Location	20° 25′ N, 85° 55′ E	21° 33′ N, 88° 15′ E	20° 75′ N 86 ° 85′ E
pH	6.53 ± 0.53^{c}	7.55 ± 0.21^{a}	6.92 ± 0.83^{b}
EC (dS m^{-1})	0.51 ± 0.02^{c}	4.11 ± 0.14^{b}	10.53 ± 0.74^{a}
SOC (%)	0.66 ± 0.03^{a}	0.52 ± 0.22^{b}	0.38 ± 0.06^{c}
TN (%)	0.08 ± 0.02^{a}	0.06 ± 0.03^{b}	0.03 ± 0.01^{c}
AP (kg ha^{-1})	13.21 ± 1.28^{b}	19.32 ± 0.23^{a}	12.5 ± 0.12^{b}
AK (kg ha^{-1})	223 ± 1.23^{c}	323 ± 2.63^{b}	1845 ± 2.93^{a}

Values within a row followed by the different letters are significantly different at HSD ($p \leq 0.05$); SD, Standard deviation; NRRI, National Rice Research Institute, Cuttack, Odisha; MS, Bakkhali, Sundarban,West Bengal; MB, Dangamal, Bhitarkanika, Odisha; EC, electrical conductivity; SOC, soil organic carbon; TN, total nitrogen; AP, available phosphorous; AK, available potassium.

Winogrodsky's medium (*Nitrosomonas medium*) was used to determine the nitrifier (NH_4^+ oxidizing) population (Sharma and Dangar, 2016). Each Petri plate was kept for incubation at 30°C for 25–30 days and then a sulfanilic acid reagent was flooded into it to observe the pink colonies. Similarly, denitrifier (NO_3^- reducing) bacterial population was counted by using Winogrodsky's medium where sodium or potassium nitrate was used instead of ammonium sulfate. Each Petri plate was incubated for 3 days at 30°C and sulfanilic acid reagent was poured into it to observe the appearance of pink colonies and these were counted.

The population of phosphate-solubilizing bacteria (PSB) was counted by using a calcium phosphate agar medium. The diluted soil samples were spread plated on plates and kept for incubation for 3 days at 30°C and the halo zone colonies were counted. A *Thiobacillus* medium was used to determine the population of sulfur-oxidizing bacteria after incubating the plate with the diluted soil sample for 7 or more days at 30°C. Black/brown colonies that appeared on the plate were counted.

Oligotrophic (OL) and copiotrophic (CO) bacterial populations were determined using tryptone soya yeast extract medium (Ochs et al., 1995) and copiotrophic isolation medium, respectively. Petri-plates were spread plated with diluted soil samples and kept for incubation for 3 days at 30°C. The brownish color colonies were counted as CFU g^{-1} soil. Jensen's medium was used to assess the asymbiotic nitrogen-fixing bacterial population after inoculating the plates with diluted soil samples and then kept for incubation for 4 days at 30°C. The colonies that appeared transparent on the plates were counted and transformed into CFU g^{-1} soil.

Community-Level Substrate Utilization Patterns Analysis Using Biolog-Ecoplate

In a 250 ml flask, fresh soil, equivalent to 10 g dry weight was taken from each MS, MB, and NRRI paddy soils. Then, 100 ml of distilled water was added and placed on a shaker at 250 rpm for 30 min. Final diluted (10^{-3}) soil suspension (150 µl) was added in 93 wells of Biolog ecoplate® (Biolog, Hayward, CA, United States), containing 31 kinds of C sources with three replications out of 96 wells. Whereas, 150 µl of sterile water was added in the remaining 3 wells (did not contain any C-source), designated as control. The eco plates were then incubated at 25°C for 24, 48, 72, 96 h, and the change of color that developed after the utilization of C sources by microorganisms was measured at an absorbance of 590 nm in Microlog 4.01 (Biolog, Hayward, CA, United States).

Determination of the Total Metabolic Activity of Soil Microorganisms

Average well color development (AWCD) for all C-sources was calculated to evaluate the total microbial activity in MS, MB, and NRRI paddy soils (Li F. et al., 2013; Kumar et al., 2017; Manjunath et al., 2018; Pradhan et al., 2019; and Kumar et al., 2020b).

$$\mathrm{AWCD} = \left[\sum (\mathrm{C} - \mathrm{R})/31\right] \quad (1)$$

Where C represents the OD (optical density) value of 31 reaction wells, and R represents the OD value of the control. The AWCD reflects the utilizing trend of different C-sources by microorganism (Choi and Dobbs, 1999).

Analysis of Utilization Pattern of Carbon Sources and Functional Diversity of Soil Microorganisms

Determination of the functional soil microbial diversity index utilizing C-sources expressed by Shannon–Weaver index (H), which is used to calculate diversity indices of the microbial community and was quantified by the formula:

$$\mathrm{H} = -\sum \mathrm{p_i} \ln \mathrm{p_i} \quad (2)$$

Where p_i is the ratio of the relative OD (absorbance) value (C-R) of No. i hole to the sum of relative OD values of all holes of the Biolog Eco-plates.

McIntosh index (U) was calculated by the formula:

$$\mathrm{U} = \sqrt{\sum (\mathrm{ni})^2} \quad (3)$$

By subtracting the OD value of the control well from each of the C-source, the relative absorbance value i.e., n_i is derived (Magurran, 1988; Wei et al., 2011; Gu et al., 2018).

Determination of Metabolic Fingerprints of Soil Microorganisms

Principal component analysis (PCA) was used to analyze the metabolic activities of soil microorganisms. Optical density (OD) values recorded in 31 kinds of C-sources utilized by the soil microbial community were used to assess the multi-element vectors (Ma et al., 2006). Six major groups of C-utilizing microbial communities were separated as per the methodology

TABLE 2 | Microbial biomass carbon and enzyme activities of soil from conventional and mangrove-converted rice areas.

Paddy Soil	MBC	DHA	FDA	UR	ACP	ALP
NRRI	615.94^{a} (4.01)	43.50^{a} (2.23)	23.57^{a} (0.89)	144.40^{a} (1.66)	73.36^{a} (2.04)	48.89^{a} (1.43)
MS	472.77^{b} (10.15)	24.76^{b} (1.47)	3.64^{b} (0.09)	142.82^{a} (3.51)	23.17^{b} (1.02)	37.81^{b} (1.54)
MB	223.96^{c} (11.57)	11.39^{c} (0.66)	2.07^{b} (0.07)	131.50^{b} (2.66)	28.25^{b} (1.96)	16.29^{c} (1.08)

Values within a column followed by the different letters are significantly different at HSD (p ≤ 0.05). Values in parentheses indicate standard deviation. NRRI: National Rice Research Institute, Cuttack, Odisha; MS: Bakkhali Sundarban, West Bengal; MB: Dangamal, Bhitarkanika, Odisha; MBC: Microbial biomass carbon (μg MBC $g^{-1}$of soil); DHA: Dehydrogenase (μg TPF g^{-1} soil h^{-1}); FDA, Fluorescin diacetate (μg FDA g^{-1} soil h^{-1}); UR:Urese (mg Urea g^{-1} soil h^{-1}); ALP: Alkaline phosphatase (μg p-nitrophenol g^{-1} soil h^{-1}); ACP: Acidic phosphatase (μg p-nitrophenol g^{-1} soil h^{-1}).

TABLE 3 | Microbial populations (Log CFU g^{-1}) of soil from conventional and mangrove-converted rice areas.

Paddy Soil	HAB	AC	F	ASNF	NI	DNF	PSB	SOB	CO	OL
NRRI	7.52^{ab}	4.02^{c}	4.01^{a}	5.67^{a}	4.33^{b}	4.86^{a}	5.81^{a}	5.27^{a}	4.39^{a}	5.16^{a}
MS	7.47^{b}	4.85^{a}	3.56^{b}	5.26^{a}	4.74^{ab}	4.91^{a}	5.93^{a}	5.62^{a}	4.79^{a}	5.56^{a}
MB	7.62^{a}	4.34^{b}	3.03^{c}	5.67^{a}	4.83^{a}	4.79^{a}	6.04^{a}	5.59^{a}	4.64^{a}	5.44^{a}

Values within a column followed by the different letters are significantly different at HSD (p ≤ 0.05). Log CFU g^{-1} soil: log transform value of colony forming unit per gram soil; HAB: hetrotrophic aerobic bacteria; AC: actinomycetes; F: fungi; ASNF: asymbiotic nitrogen fixing bacteria; NI: nitrifing bactria; DNF: denitrifing bactria; PSB: phosphate solubilizing bacteria; SOB: sulfur oxidizing bacteria; CO: copiotrophs; OL: oligotrophs.

of Insam et al. (1996) and then analyzed for biplot-PCA to correlate with other soil parameters.

Statistical Analysis

Online statistical computing software of NARS, Indian Agricultural Statistics Research Institute, New Delhi, India, was used to analyze the data (http://www.iasri.res.in/sscnars). Descriptive statistics like one-way ANOVA was used to access the variance between means of analyzed parameter among the sampling sites and where significant *F* value was observed. Difference between individual means was tested using Tukey HSD (Honestly significant difference) at a 5% level of significance. The principal coordinate analysis (PCoA) by Bray–Curtis distance-based redundancy analysis (dbRDA) while the Vegan package in *R* software version 3.5.0 was used to assess the soil parameters with different treatments. The sample size was taken and analyzed as per Chowdhury et al. (2021b).

RESULTS

Soil pH and Nutrient Contents

Soil pH was significantly ($p < 0.05$) higher in mangrove-converted paddy soils of MS (7.55) and MB (6.9) compared to NRRI paddy soil (NRRI) (6.5) (**Table 1**) and natural mangroves of MS and MB (**Supplementary Table S1**). Similarly, soil organic carbon (SOC) was significantly ($p < 0.05$) lower in MS (0.52%) and MB (0.38%) compared to NRRI (0.66%) (**Table 1**) and the natural mangroves of MS and MB (**Supplementary Table S1**). EC was recorded higher in natural mangroves of MS and MB compared to MS, MB, and NRRI paddy soils (**Table 1**; **Supplementary Table S1**). Whereas, available phosphorus (AP) and available potassium (AK) were significantly ($p < 0.05$) higher in mangrove-converted paddy soils (AP higher in MS and AK higher in MB) compared to NRRI (**Table 1**).

Microbial Biomass Carbon and Soil Enzymatic Activities

Soil microbial biomass carbon (MBC) ranged from 223.9 μg g^{-1} to 615.9 μg g^{-1} in all three studied locations. MBC was significantly ($p < 0.05$) higher in NRRI than MS and MB. The dehydrogenase activity (DHA) in NRRI was 43.5 μg g^{-1}, whereas it was 24.7 μg g^{-1} and 11.3 μg g^{-1} in MS and MB, respectively. An almost similar trend in the result found in other soil enzyme activities such as urease (U), acidic phosphatase (ACP) and alkaline phosphatase (ALP), and these were recorded higher in NRRI paddy soil (144.4 mg g^{-1}, 73.3 μg g^{-1}, and 48.8 μg g^{-1}, respectively) compared to MS and MB (**Table 2**).

Soil Microbial Population Dynamics

All soil microbial populations (Heterotrophic aerobic bacteria, asymbiotic nitrogen-fixing bacteria, nitrifying bacteria, denitrifying bacteria, phosphate solubilizing bacteria, sulfur-oxidizing bacteria, copiotrophs, and oligotrophs) except actinomycetes and fungi were found non-significant among NRRI, MS, and MB sites. Significantly ($p < 0.05$) higher actinomycete counts were obtained in MS followed by MB and NRRI (MS > MB > NRRI), whereas the fungal population was recorded highest in NRRI followed by MS and MB (NRRI > MS > MB) (**Table 3**). In undisturbed mangrove soils of MS and MB, the population of HAB, NI and PSB were found lower compared to converted MS and MB, whereas the population of AC showed dominance under undisturbed MS (**Supplementary Table S1**).

Soil Microbial Community and Functional Diversity

A significantly ($p < 0.05$) lower value of AWCD and rate of AWCD were found in MB compared to MS and NRRI (MB < MS < NRRI) during the 24–96 h incubation period (**Figure 1**). Similarly, the diversity indices such as Shannan–Weaver and

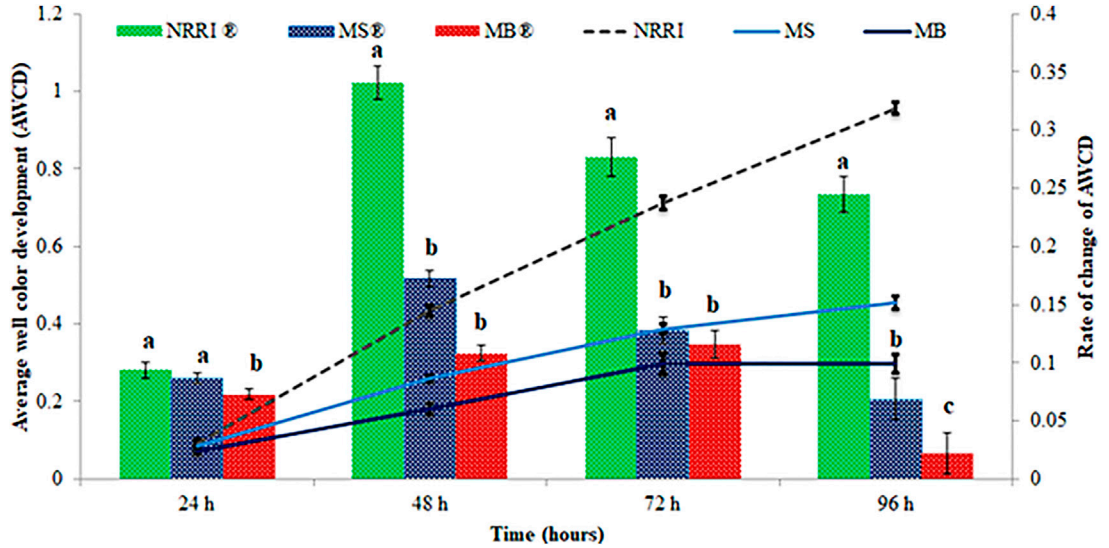

FIGURE 1 | Variation of average well color development (AWCD) and rate of AWCD in mangrove-converted and conventional paddy soils. NRRI: National Rice Research Institute, Cuttack, Odisha; MS: Bakkhali, Sundarban, West Bengal; MB: Dangamal, Bhitarkanika, Odisha. ® indicates the rate of change of AWCD. Lines above the bars represent means ± standard deviation. Different letters above the bars indicate significant among the treatments at Tukey HSD ($p \leq 0.05$).

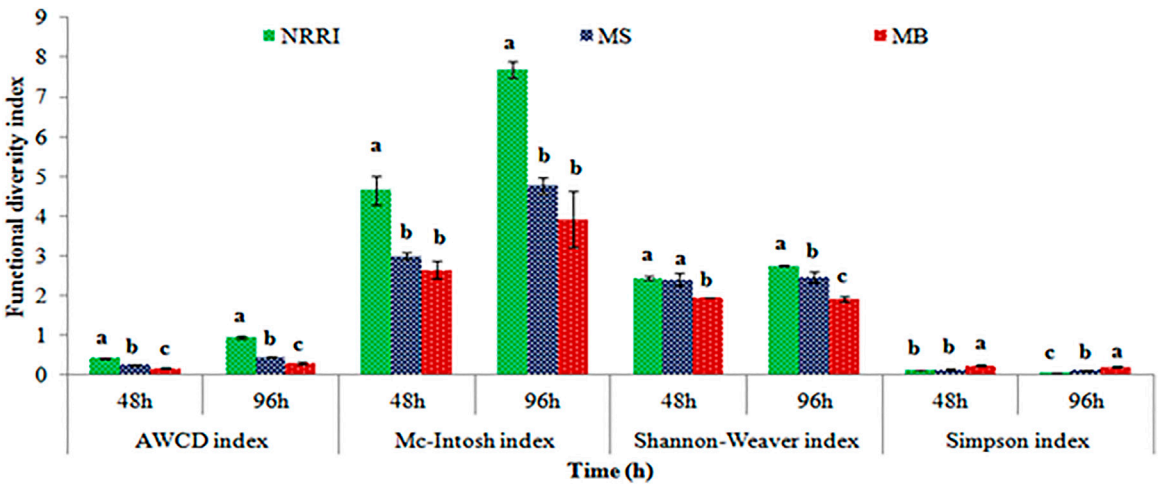

FIGURE 2 | Variation of different functional diversity indices in mangrove-converted and conventional paddy soils. NRRI: National Rice Research Institute, Cuttack, Odisha; MS: Bakkhali, Sundarban, West Bengal; MB: Dangamal, Bhitarkanika, Odisha. Lines above the bars represent means ± standard deviation. Different letters above the bars indicate the treatments at Tukey HSD ($p \leq 0.05$).

McIntosh indices were also found lower in MB compared to MS and NRRI (NRRI > MS > MB), whereas the Simpson index showed the opposite trend of Shannan–Weaver and McIntosh indices (NRRI < MS < MB) (**Figure 2**).

Utilization Pattern of C- Sources by Soil Microbes in NRRI, MS, and MB

A biplot analysis of the parameters obtained from NRRI, MS, and MB soils was shown in the ordination plane (**Figure 3**), in which the PCA explained a total variance of 97.22%, with principal component 1 (PC1) representing 62.37% and principal component 2 (PC2) representing 34.85% variances, respectively. The PCA showed that the corresponding projective points of six major C groups namely phenolic compounds, polymers, amines, and amino acids; carbohydrates; carboxylic compounds lay at the first, second, and fourth quadrant, respectively (**Figure 3**), out of which carbohydrates consumption was found highest in NRRI soils compared to MS and MB (**Figure 4**). The phenolic

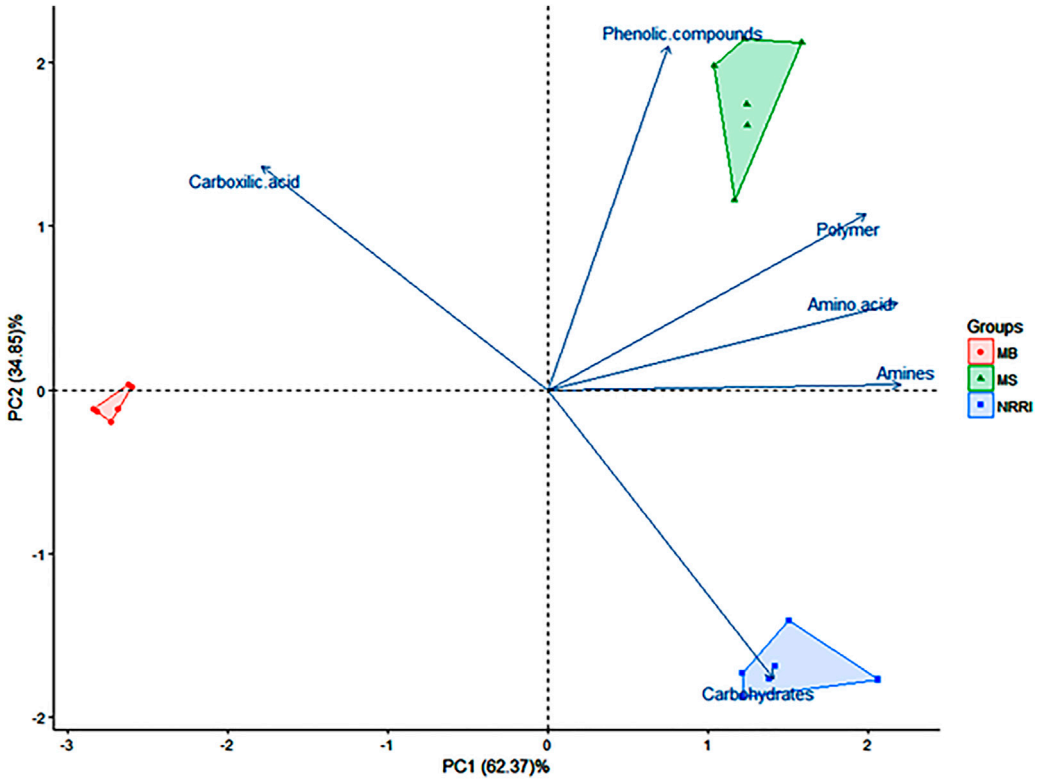

FIGURE 3 | Biplot analysis based on 48 h biolog data indicating separation of three treatments of mangrove-converted and conventional paddy soils. NRRI: National Rice Research Institute, Cuttack, Odisha; MS: Bakkhali, Sundarban, West Bengal; MB: Dangamal, Bhitarkanika, Odisha. Values in parentheses indicate percentage contribution by PC1 and PC2.

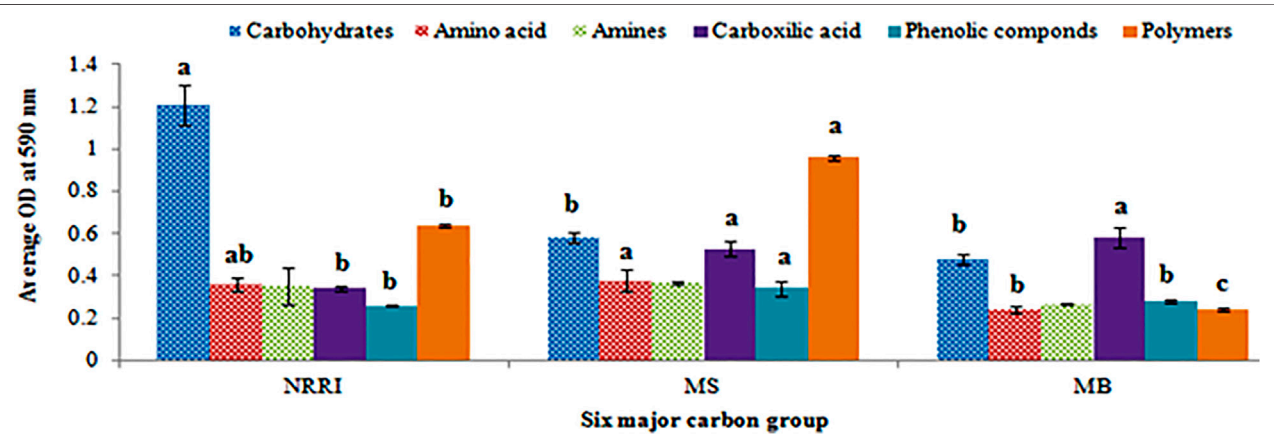

FIGURE 4 | Microbial consumption of six major groups of carbon sources of soil in mangrove-converted and conventional paddy soils. NRRI: National Rice Research Institute, Cuttack, Odisha; MS: Bakkhali, Sundarban, West Bengal; MB: Dangamal, Bhitarkanika, Odisha. Line on bars represent means ± standard deviation. Different letters indicate the significant differences in the six major groups of carbon sources utilized by the microbial community among the treatments at Tukey HSD ($p \leq 0.05$).

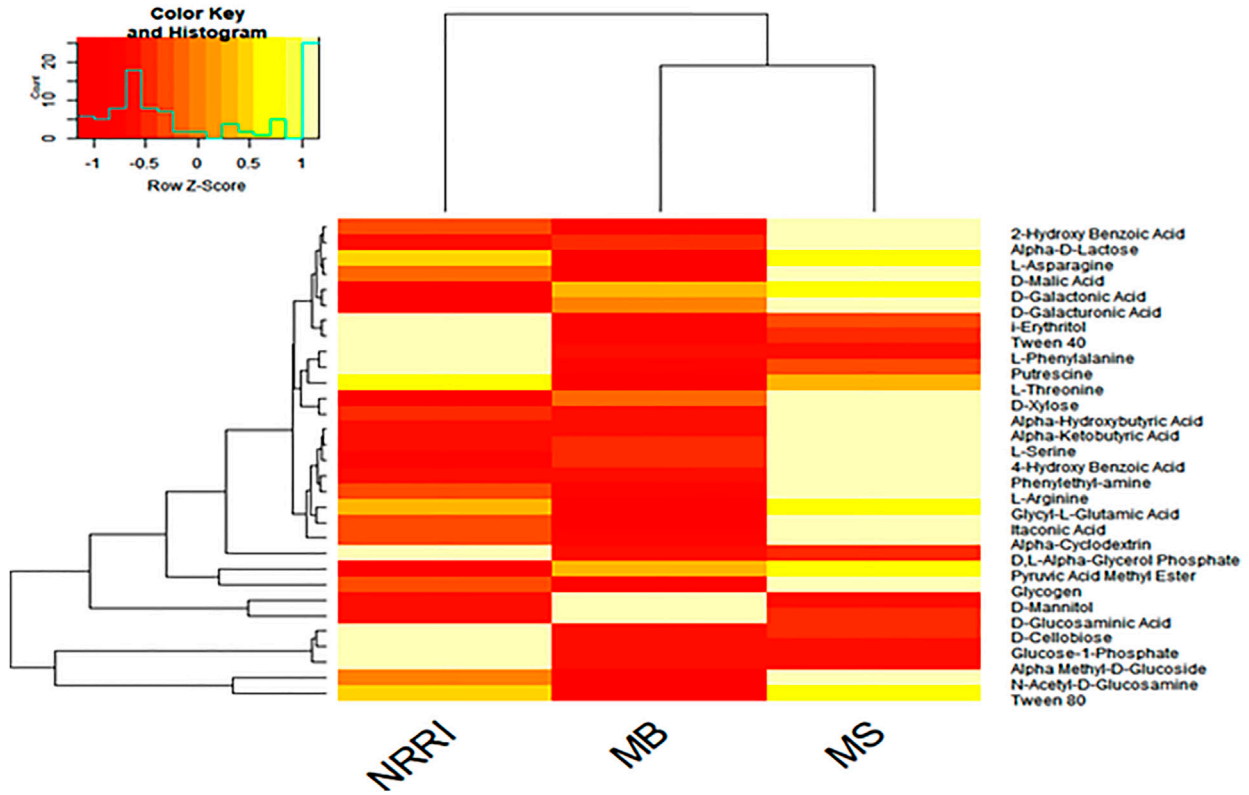

FIGURE 5 | Heatmap of carbon source utilization by the microbial community in conventional paddy soil (NRRI) and mangrove-converted paddy soil (MS and MB). NRRI: National Rice Research Institute, Cuttack, Odisha; MS: Bakkhali, Sundarban, West Bengal; MB: Dangamal, Bhitarkanika, Odisha. Light yellow color shows higher and dark red color show lower carbon utilized by the soil microbial community.

compounds were positively correlated with MS whereas the carboxylic compound was positively correlated with MB (**Figure 4**). Polymer compounds were utilized efficiently in the MS soil (**Figure 4**).

A heat map analysis showed the differentiation of MS and MB from NRRI soil based on the utilization pattern of 31 kinds of C-source by soil microbes. Three C-sources (D-Cellobiose, Glucose-1-phosphate, and α-Methyl-D-Glucoside) were consumed very little by soil microbes present in MS and MB, whereas efficient consumption of these three C-sources was observed in NRRI (**Figure 5**).

Correlation of MS, MB, and NRRI Based on Physico-Chemical and Biological Parameters

A biplot analysis of the parameters obtained from NRRI, MS, and MB was shown in the ordination plane (**Figure 6**), in which the PCA explained a total variance of 84.17%, with the principal component 1 (PC1) representing 61.80% and principal component 2 (PC2) representing 22.37% variances, respectively. Correlation among the quantified variables demarcated the lines in the same direction being more closely related. Biplot depicts FDA, ACP, and DHA were positively correlated with NRRI (**Figure 6**). AP, AC, and pH were positively correlated with MS, whereas EC and PSB were positively correlated with MB (**Figure 6**).

DISCUSSION

Individual reports on the variation of the soil microbial community under sub-humid tropical mangroves and conventional rice ecology were plenty; however, studies on the conversion of mangrove vegetation into rice cultivation and its effect on the soil microbial community are very limited. Therefore, the present study was initiated to understand the functional microbial community of paddy soil under these habitats. The findings of the present investigation suggested the lower functional microbial diversity (AWCD and rate of change of AWCD) in MS and MB compared to conventionally grown rice under sub-humid tropical conditions. Out of six major C-sources, the majority of the microbes' under NRRI utilized carbohydrates (a simpler form of sugars) compared to MS and MB, which might be one of the reasons to have a higher diversity of the microbial community in this condition (Huang et al., 1998; Li et al., 2007; Haque et al., 2013; Kumar et al., 2017). In contrast, MS and MB harbored microbial communities consumed complex C-sources such as phenolic compounds, carboxylic compounds, and polymers. Most of the microbes might show a metabolic

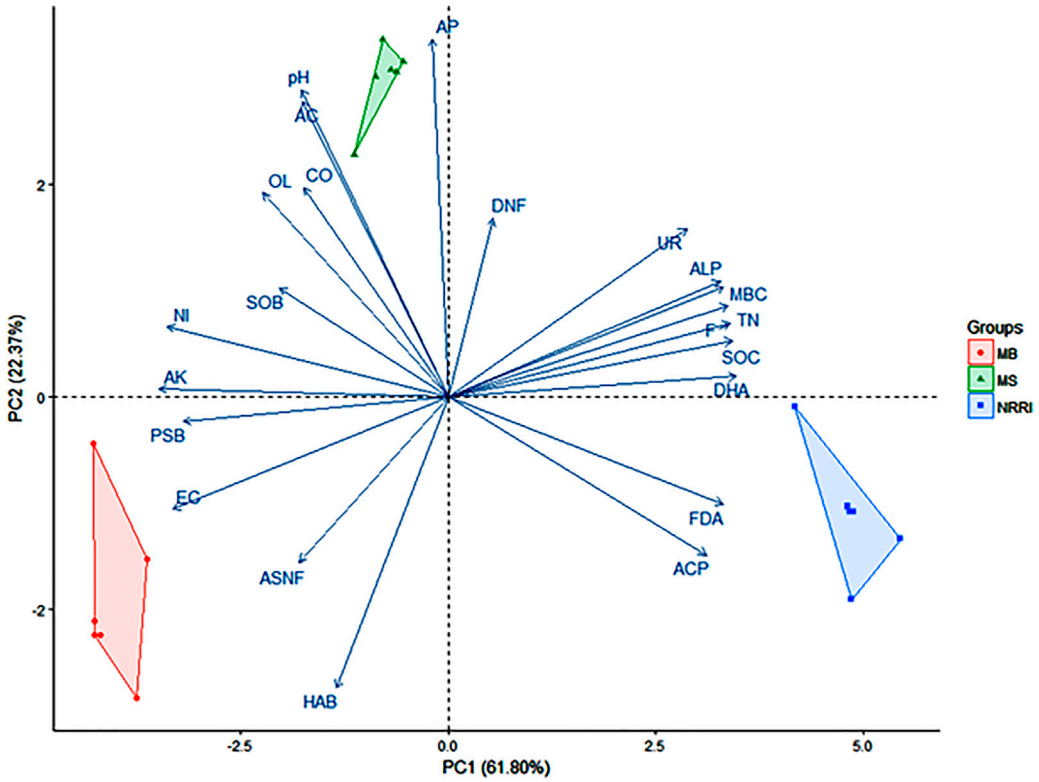

FIGURE 6 | Biplot analysis of physico-chemical and biological factors in mangrove-converted and conventional paddy soils. NRRI: National Rice Research Institute, Cuttack, Odisha; MS: Bakkhali, Sundarban, West Bengal; MB: Dangamal, Bhitarkanika, Odisha; MBC: microbial biomass carbon; DHA: dehydrogenase; FDA: fluorescein diacetate; UR: urease; ALP: alkaline phosphatase; ACP: acidic phosphatase; TN: total nitrogen; SOC: soil organic carbon; AK: available potassium; AP: available phosphorus; F: fungi; ASNF: asymbiotic nitrogen fixers; HAB: heterotrophic aerobic bacteria; PSB: phosphate solubilizing bacteria; NI: nitrifiers; SOB: sulfur oxidizing bacteria; OL: oligotrophs; CO: copiotrophs; AC: actinomycetes; DNF: denitrifiers. Values in parentheses indicate percentage contributions by PC1 and PC2.

versatility which permits their existence and survivability under mangrove-converted paddy compared to conventional paddy soil. Carbon utilization pathways in microbes have been investigated for the last 60 years in order to better understand the choice of preferential C-sources utilized by certain bacterial communities in relation to the shift of environmental conditions (Guimarães, 2012; Beisel and Afroz, 2016) as indicated in our study.

Shannon–Weaver and McIntosh indices also showed similar trends of microbial diversity (NRRI > MS > MB), whereas the opposite trend was found in the case of the Simpson index. Shannon–Weaver and McIntosh's indices are powerful tools to determine the species' richness and evenness in diverse ecosystems (Shannon and Weaver, 1949; McIntosh et al., 1967; DeJong, 1975; Kennedy and Smith, 1995; Harch et al., 1997). In the present study, lower species' richness and evenness were found in MS and MB compared to NRRI, and for that reason, the functional diversity of soil microbes was significantly lower in MS and MB. Another possible reason to increase microbial richness in NRRI might be due to the frequent application of organic manures and fertilizers (Dong et al., 2014; Kumar et al., 2017). Besides, in NRRI, rice cultivation was being practiced since 1946 which promoted to build up more organic C at NRRI than MS and MB, possibly favoring a higher species' richness of bacteria, particularly the carbohydrate utilizers in this condition (Danovaro and Fraschetti, 2002; Pinhey and Tebbs, 2022; Underwood et al., 2022). The Simpson index indicates the dominance of the species community in a particular ecosystem which is inversely proportional to the McIntosh index which is corroborated with our findings.

PCA analysis shows that enzyme activities such as acid phosphatase, dehydrogenase, and fluorescein diacetate are positively correlated with NRRI compared to MS and MB. Suitable soil pH (slightly acidic) favors the production of acidic phosphatase (Dick and Tabatabai, 1984; Gu et al., 2009) in NRRI which helps to increase heterotrophic aerobic bacteria (HAB) by utilizing the different carbohydrate sources in this condition (Kavadia et al., 2007; Shu et al., 2012; Roper and Gupta, 2016). Fluorescein diacetate also showed a positive correlation with NRRI, indicating higher microbial richness as FDA hydrolysis correlates with microbial indices such as ATP content, biomass, and cell density (Jiang et al., 2016). Previous reports indicated that FDA hydrolysis has been found to be significantly correlated with microbial biomass in pure and mixed microbial cultures, pastures, and cultivated soils, and soil amended with municipal refuse, and could be used as an

alternative estimate of the content and size of soil microflora (Green et al., 2006; Sánchez-Monedero et al., 2008; Wang et al., 2018).

MS harbored higher CFU of actinomycetes, oligotrophs, sulfur-oxidizing bacteria, and nitrifiers which showed a positive response to available phosphorus (AP), urease, and soil pH. Alkaline pH and higher AP in MS primarily favored the growth of these microbes (Bandyopadhyay and Sarkar, 1987; Das et al., 2011; Halder et al., 2015). The present study also showed the higher CFU of phosphate-solubilizing bacteria in MB compared to MS and NRRI. Reports indicated that the higher phosphate solubilizing microbial diversity occurred in mangrove soil containing a lower amount of AP (Adnan et al., 2017). Researchers also revealed that P was the limiting factor of the microbial diversity and productivity of mangroves ecosystems (Reich and Oleksyn, 2004; Lovelock et al., 2007; Krauss et al., 2008). The present study showed that MB was positively correlated with electrical conductivity (EC). Interestingly, EC was found higher in undisturbed MS and MB which might have hampered the growth of microbial populations such as HAB, NI, and PSB compared to converted MS and MB (Mishra et al., 2012; Chatterjee et al., 2015). The population of AC was more in undisturbed MS than converted MS, possibly due to being halophilic in nature (Ballav et al., 2015). The possibility of high EC might be due to less saline soil as alkalinity is inversely proportional to EC (Mohd-Aizat et al., 2014). Moreover, salinity levels might alter the microbiome under mangrove and mangrove-converted paddy soils, consequently influencing mangrove production (Chambers et al., 2016).

The converted mangroves of both MS and MB showed a negative response to FDA and DHA, this might be due to poor microbial diversity as microbial indices such as biomass, cell density, and ATP content are positively correlated with FDA which might have decreased due to anthropogenic activities in the wetlands of the mangrove ecosystem (Jiang et al., 2016). Conjoining all the results, we found that all the three sites *viz*., paddy soils of NRRI and converted mangrove paddy soils of MS and MB are distinct ecosystems that differ from each other in terms of microbial diversity, enzymatic, and soil physico-chemical parameters. However, a detailed quantification of biotic (plant taxonomy, anatomy, and sediment fauna) and abiotic (temperature, salinity, tidal amplitude and frequency, and pollution level) variables that can influence the composition and functions of the microbiome is required to achieve a mechanistic understanding under MS and MB compared to NRRI. Overall, our results indicated that rice cultivation under MS and MB alters the microbial diversity compared to NRRI, which might be due to severe anthropogenic activities that gradually destroyed these habitats.

CONCLUSION

The present study concludes that anthropogenic practices in the coastal wetlands of the mangroves of Sundarban and Bhitarkanika have hindered the microbial diversity of the mangrove ecosystem. However, NRRI, which is a completely rice–rice system where cultivation of rice is being carried out over 70 consecutive years, showed increased microbial richness along with enzymatic and physico-chemical parameters than MS and MB. The decreased concentrations of these parameters in MS and MB might be due to the conversion of these areas into rice cultivating lands. Therefore, the findings of this study suggested the deterioration in the rich mangrove diversity might be due to its conversion to rice cultivation by anthropogenic activities.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

UK framed the notion and was overall in charge of this manuscript preparation. UK and MK collected literature, analyzed data, and drafted the manuscript. PP and AN edited the manuscript. All contributors discussed the outcomes and added them to the final document. All authors have studied and approved the in-print version of the article.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.858028/full#supplementary-material

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