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Wetland conversion to cropland alters the microbes along soil profiles and over seasons

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ABSTRACT

Soil microbes drive biogeochemical cycles of carbon (C) and nutrients, and land conversion alters soil microbes and thus, affects C and nutrient cycling at the ecosystem level. To evaluate the impacts of wetland reclamation on microbes along soil profiles and over seasons, soil cores (0–100 cm) were collected from a natural wetland and an adjacent cropland that has been continuously cultivated for 23 years in the Sanjiang Plain, northeastern China. Wetland conversion to cropland generally homogenized the microbial abundance along the soil profiles in four seasons (May of spring, July of summer, October of autumn, and December of winter), while the vertical homogenization was the strongest in summer and weakest in winter. After 23 years of cultivation, the abundances of fungi and bacteria in surface soils were significantly reduced by approximately 90% and 80%, respectively, whereas the bacterial abundances increased and fungal abundances decreased in middle and deep soils, suggesting that cultivation impacts on microbial community structure varied along soil layers. Compared to the wetland, total phospholipid fatty acids in the middle and deep soils of the cropland were enhanced by approximately 60–367% in autumn and winter and 30–137 % in spring and summer. Wetland reclamation suppressed the microbial diversity in the surface soils in winter, spring, and summer but stimulated that in autumn, indicating robust enhancements on microbial diversity by the inputs of fresh litter C. The quantifications of microbial abundance and community structure showed the non-uniform impacts of wetland reclamation on microbes along the soil profile and over seasons, which provides valuable information for benchmarking models in simulating microbial roles on C cycling in deep soils at the seasonal scale.

1. Introduction

Wetlands occupy approximately 6% of the land surface on Earth but store more than 12% of the global carbon (C) (Ferrati et al. 2005). They play indispensable roles in global biogeochemical cycles (Erwin 2009) and provide numerous ecosystem services, including flooding prevention and habitats for wildlife (Houlahan et al. 2006). However, more than half of natural wetlands have disappeared since the Industrial Revolution, and approximately 26% of the global wetlands have been converted to agricultural land (Zedler and Kercher 2005). The conversion of wetland to cropland has led to substantial loss of soil C (Post and Kwon 2000) and dramatic alternations in soil elements, soil texture, and pH (Edwards et al. 2015; Gao et al. 2010b), which further affects soil microbes and ecosystem productivity (Karlen et al. 1997).

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Land conversion strongly influences soil microbial properties, including microbial diversity (Fierer et al. 2003), microbial biomass (Anderson et al. 2017), microbial community (Rodrigues et al. 2013), and microbial metabolic quotient (Xu et al. 2017). For example, Huang et al. (2008) observed an enormous loss of microbial biomass in marshland owing to wetland reclamation; Song et al. (2012) reported a greater than 80% reduction of soil microbial biomass C (MBC) at a depth of 0 ~ 20 cm after the wetland reclamation in the Sanjiang Plain, China. However, the impacts of land conversion on soil microbial diversity are controversial. Allan et al. (2014) and Sala et al. (2000) reported a reduction in microbial diversity after the conversion of wetland to cropland, while Rodrigues et al. (2013) found homogenized species composition and no reduction in microbial diversity. Considering the vital roles of soil microbes in driving nutrient cycling and affecting vegetation productivity (Schnitzer et al. 2014), the impacts of reclamation on microbial abundance, composition, and diversity along soil profiles are critically important but remain under-investigated. Despite the facts that most previous studies focused on microbial properties in the surface soil of 0 ~ 30 cm, soil microbes in the subsurface soil of 30 ~ 100 cm have substantial impacts on nutrient biogeochemistry as well (Xu et al. 2013, 2017; He et al. 2020; Fierer et al. 2003). Understanding the wetland reclamation impacts on soil microbes along entire soil profiles is critical for enhancing our predictability of soil microbes under a changing environment.

Seasonality is a fundamental mechanism for microbes to remain resilient (He et al. 2021). Seasonal variations of microbial properties have been reported widely. For example, soil MBC and microbial biomass nitrogen (MBN) exhibited strong seasonality in the northeastern U.S. grassland (Corre et al. 2002). Microbial abundance and activities were observed the highest in summer and the weakest in winter in some croplands and wetlands (Boadella et al. 2021; Lepcha et al. 2020). The microbial seasonality is mainly attributed to the variation in substrate availability over seasons (Kaiser et al. 2010), primarily controlled by root exudates, nutrient absorption, and litter production (Kaiser et al. 2010). In addition, microbial properties are also regulated by soil pH (Fierer et al. 2006), temperature (Barcenas-Moreno et al. 2009; Yuan et al. 2021a), moisture (Fierer et al. 2003, Yuan et al. 2021b), and organic C (Xu et al. 2014). The seasonal variations in these soil properties can cause inconsistent responses of microbes to wetland reclamation over seasons (Boadella et al. 2021; Kaiser et al. 2010). However, most studies on the impacts of land conversion on microbial properties focused on the average performance across seasons (Allan et al. 2014; Sala et al. 2000; Huang et al. 2008; Song et al. 2012), and the land conversion impacts among seasons remained understudied.

In this study, the microbial abundance, microbial community structure, and diversity were measured along 100 cm soil profiles in the autumn, winter, spring, and summer from a natural wetland and an adjacent 23-year cultivated cropland in the Sanjiang Plain, northeastern China. The land conversion impacts on soil microbes were quantified, and the associations between microbial properties and soil chemical parameters along soil profiles were explored to a depth of 100 cm. We hypothesized that: 1) strong seasonal variations in meteorological factors lead to microbial seasonality, and the seasonal amplitude declines as the soil depth increases; 2) the impacts of wetland conversion to cropland are the strongest in the summer and the weakest in winter; and 3) environmental factors, such as temperature and C density, predominantly control the microbial responses to wetland conversion to croplands.

2. Material and methods

2.1. Study site and soil sampling

This study was conducted at the Sanjiang Experimental Station of Wetland Ecology (133°31′ E, 47°35′ N); the Sanjiang Plain in northeastern China features the most extensive freshwater wetlands in China (Shi et al. 2020; Song et al. 2009; Zhu et al. 2021). At the study site, the natural wetland was reclaimed for a soybean plantation in 1996 (Zhu et al. 2021). Soybean is an annual crop with a growing season from May to October, and the soybean field has received no fertilization over the past 23 years but was tilled on a yearly basis. There is a 30–35 cm water layer covered on wetland's surface, which freezes in the winter. Along the soil profile, the 0 ~ 70 cm soil profile is dominated by meadow soils, while 70 ~ 100 cm is white territory soils (Wang et al. 2003). The soil texture along the soil profile is silty loam (Table S1) based on the USDA soil texture classification (Kyebogola et al. 2020).

Soil cores were collected from the wetlands and croplands during October 10–12, 2019, December 27–29, 2019, May 13–15, 2020, and July 19–21, 2020, representing autumn, winter, spring, and summer, respectively. During each season, three 100-cm soil cores were randomly excavated in a soybean field (133°30′ E, 47°36′ N) and the natural wetland plot (133°30′ E, 47°35′ N). Twenty-four cores were extracted in total. Those soil cores were divided into 10-cm sections (0 ~ 10, 10 ~ 20, 20 ~ 30, 30 ~ 40, 40 ~ 50, 50 ~ 60, 60 ~ 70, 70 ~ 80, 80 ~ 90, and 90 ~ 100 cm). Half of the soil samples were stored at 4℃ for measuring soil total carbon (TC), total nitrogen (TN), total phosphorus (TP), total sulfur (TS), pH, moisture, MBC, MBN, microbial biomass phosphorus (MBP), and microbial biomass sulfur (MBS). The other soils were stored at − 80℃ for phospholipid fatty acids (PLFA) analysis. The soils of 0 ~ 30 cm were defined as topsoil (Xu et al. 2013, 2017; He et al. 2020). According to the distribution of white territory soil (Wang et al. 2003) and the 70 cm as the deepest frozen soils at our study site (Zhu et al. 2021), we defined 30 ~ 70 cm as middle soils and 70 ~ 100 cm as deep soils.

2.2. Measurements of soil and microbial properties

The detailed information for the measurements of the soil and microbial properties has been described in our previous study (Zhu et al. 2021). In brief, air-dried soil samples were used to measure the TC, TN, TP, TS, and soil pH, and fresh soil samples were used to measure the soil moisture, MBC, MBN, MBP, and MBS (Brookes et al. 1982, 1985; Wu et al. 1990).

The PLFA approach was adopted to quantify the abundance of soil microbes as described by Frostegard et al. (1993) and Wardle and Ghani. (1995). In total, 146 PLFAs were analyzed, and their sum was used as a proxy for total microbial biomass in soil, expressed as per g dry soil. The microbial functional groups were calculated based on a number of special PLFA markers: fungi (18:2ω6, 9c, 18:1ω9 and 18:3ω6), Gram-positive bacteria (10Me16:0, 10Me17:0 and 10Me18:0, i14:0, i15:0, a15:0, 16:0, i16:0, i17:0, a17:0, a18:0 and a19:0), Gram-negative bacteria (Cy17:0 and Cy19:0, 16:1ω7c, 16:1ω9c and 18:1ω7c), and unspecific bacteria (14:0, 17:0, 16:1ω8c, 16:1ω5c, 18:1ω8c, 16:1ω7, 16:1ω7t, 18:1ω7t, 18:1ω6c and 18:0; Vestal and White 1989; Gentsch et al. 2020; Joergensen 2021). Unspecific bacteria were defined as a microbial group calculated from PLFA markers that carry total bacterial markers but do not belong to any specific microbial groups. The PLFA markers that do not indicate any microbes were unclassified microbial groups.

2.3. Statistical analysis and calculation of microbial parameters

Statistical analyses were conducted by using the R programming (V 4.0.2, R Core Team, 2020). Duncan's multiple range test (MRT) was applied to compare the soil pH, TC, TN, TP, TS, MBC, MBN, MBP, MBS, and PLFA among the 10 soil layers for autumn, winter, spring, and summer, followed by Fisher's least significant difference (LSD) test at a 0.05 significance level. A T-test was performed for every independent variable to quantify the differences in soil and microbial properties between wetland and cropland for 10 soil layers in four seasons. One factor ANOVA test was used to compare soil and microbial properties among seasons in cropland and wetland for 10 soil layers. Three repeated measures were used for each independent variable for each soil sample.

Data were expressed as the mean ± standard deviation of three replicates.

Phospholipids are essential membrane components of all living cells, and they cannot be measured in dead cells (Zelles 1999). A previous study (White et al. 1979) indicated that the changes in PLFA patterns imply the variations in microbial community structure. As the PLFA measurements reflect microbial compositions, it has been used to quantify microbial diversity (Wander et al. 1995; Korner and Laczko 1992). The richness and evenness of the microbial community were comprehensively considered using the Shannon index (Shannon 1948), which was calculated in different soil profiles using individual PLFAs as proxies for the species. Their differences between wetland and cropland were compared to explore the impacts of land conversion on microbial diversity. To quantify the microbial responses to wetland reclamation and cultivation, we calculated the relative differences in microbial abundance in the wetland and cropland at each soil layer using Eq. (1):

$$c = \left| \frac{C_W - C_c}{C_W} \right| \times 100\% \quad (1)$$

where c is the relative difference of microbial abundance between wetland and cropland, and C_w and C_c are the microbial abundances in soils from wetland and cropland, respectively. A small c value indicates a trivial difference, while a large c value means a substantial difference between the wetland and cropland.

We used the principal component analysis (PCA) to evaluate the differences in microbial compositions between wetland and cropland for four seasons. We analyzed the abundances of three microbial groups - fungi, bacteria, and unclassified microbes. Before conducting the PCA, we standardized all the microbial data by subtracting all values by their arithmetic mean. The relative abundances of these soil microbial groups and microbial groups (i.e., Gram-positive bacteria, Gram-negative bacteria, and unspecific bacteria) were calculated for the surface, middle, and deep soils, and then a cluster analysis was conducted using the Bray method.

To investigate the controlling factors on soil microbial biomass in different soil layers, correlation analysis was carried out for soil chemical variables and microbes based on Pearson's correlation efficient. A Mantel test was conducted to evaluate the associations between fungal abundance, bacterial abundance, the concentration of total PLFAs, climatic variables, and edaphic factors. To quantify the land conversion impacts, we defined specific numerical codes to represent land use types in the study. Specifically, the wetland is set to 1, and the cropland is set to 2. Soil temperatures represented the impacts of seasons. The log–-transformation was applied to ensure the normality of data before conducting the correlation analysis.

To illustrate the vertical distributions of different microbial groups over seasons in the wetland and cropland, the cumulative soil microbial fraction of each soil layer was calculated by considering the whole concentrations of MBC, MBN, fungi, or bacteria in the 0–100 cm soil profiles to be 1. These microbial properties were then fitted against soil depth using an asymptotic Eq. (2) (Xu et al. 2013; Guo et al. 2020):

$$Y = 1 - \beta^d \quad (2)$$

where Y is the cumulative fraction of soil microbial properties from the soil surface to the depth of d in cm, and β is the fitted coefficient. A higher β value indicates a lower proportion of soil microbial biomass near the surface and vice versa.

Two PLFA ratios, cyclopropyl fatty acids: cyclopropyl precursors (CF: CP) and total saturated fatty acids: total monounsaturated fatty acids (TS: TM), have been confirmed to indicate environmental and substrate stress for the microbial groups (Knivett and Cullen 1965; Guckert et al. 1986; Lundquist et al. 1999). The conversion of unsaturated fatty acids to saturated fatty acids and the biosynthesis of cyclopropane fatty acids can improve cell survival (Brown et al. 1997; Grogan and Cronan 1997). Higher ratios suggest stronger inhibition of microbial growth (Zelles et al. 1992; Kieft et al. 1997; Bossio and Scow 1998; Law et al. 1963; Knivett and Cullen 1965; Thomas and Batt 1969). As the CF: CP and TS: TM is consistent along soil profiles, edaphic stress was used to represent both environmental and nutrient stresses.

Structural equation modeling (SEM) analyzed the multiple variables and their interactive controls on soil and microbial properties along soil depths and over seasons. First, a priori model was developed, which allowed a hypothesized causal interpretation of the linkages among soil depth, temperature, and the soil chemical and microbial properties for wetland and cropland. Models were then constructed, and the closest fit with the best modeling result from the SEM analysis was determined. In the SEM models, soil temperatures represent seasons; soil TC represents soil elements and the CF: CP ratio represents the microbial responses to environmental stresses. To quantify the changes in microbial and chemical properties in responses to wetland reclamation, we standardized their relevant parameters at each soil layer in the wetland and cropland with the Eq. (3).

$$\Delta v = \frac{V_W - V_c}{V_W} \times 100\% \quad (3)$$

where Δv is the variation of microbial and chemical variables, such as pH, soil TC, moisture, environmental stress, microbial diversity, and biomass; *Vw* represents variables of wetland soils and *Vc* for the same variables of cropland soils. The differences in microbial composition were calculated using the Bray-Curtis dissimilarity test according to the three soil microbial groups. The results of the best-fitting regression models were presented.

3. Results

3.1. Wetland reclamation impacts on soil and microbial properties

Wetland reclamation had various strong impacts on soil chemical and microbial properties across soil depths and over seasons (Table S1 - S7; Fig. S1). Soil TC significantly decreased with the soil depth ($p < 0.05$) for both wetland and cropland. After wetland reclamation, a dramatic loss of soil TC was observed, declining from 163.3 ± 12.1 to 5.4 ± 2.1 g/kg in the wetland to 24.0 ± 3.4 to 3.5 ± 1.5 g/kg in the cropland (Table S1 – S3). Soil pH increased along soil depths for both land types with the higher pH in cropland. The soil pH of the wetland was higher in autumn (5.4 ± 0.1 to 5.6 ± 0.1) and winter (5.3 to 6.1 ± 0.1) than in spring (5.1 to 5.6 ± 0.1) and summer (4.8 to 5.2 ± 0.1) ($p < 0.05$), while the highest soil pH in the cropland was observed in winter (5.9 to 6.2 ± 0.1).

The total PLFA decreased with soil depths ($p < 0.05$) in both wetland and cropland (Table S5). For example, total PLFA in the winter (1.4 ± 0.1 to 74.4 ± 5.0 nmol/g in the wetland and 3.8 ± 0.3 to 25.4 ± 6.1 nmol/g in the cropland) was significantly lower than that in the autumn, spring, and summer in both the wetland (11.2 ± 2.0 to 563.3 ± 104.7, 4.9 ± 2.0 to 508.6 ± 177.7, and 3.8 ± 1.6 to 421.9 ± 243.4 nmol/g, respectively) and cropland (8.3 ± 2.4 to 100.3 ± 12.6, 4.9 ± 2.9 to 77.2 ± 19.2, and 11.7 ± 6.0 to 60.2 ± 17.8 nmol/g, respectively) ($p < 0.05$). The impacts of wetland reclamation on microbial biomass were dependent on soil depths. In particular, the MBC and MBN in the surface soils decreased by 31% − 62% ($p < 0.05$) after wetland conversion to cropland; however, the MBC and MBN in the middle and deep soils increased by approximately 100–200%.

Microbial diversity decreased along the soil profiles and varied among seasons (Fig. 1). For both the wetland and cropland, the microbial diversity in the surface soils was the lowest in the winter (0.68 to 2.26 in wetland and 0.27 to 1.51 in cropland) and the highest in autumn (1.06 to 3.47 in wetland and 1.57 to 3.43 in cropland). It showed that the microbial diversity of the surface soils for each land use type was similar in the spring (0.55 to 3.09 in wetland and 0.14 to 2.07 in cropland) and summer (0.55 to 2.96 in wetland and 0.3 to 1.51 in cropland). However, the seasonal variations in the middle and deep soils were relatively weak

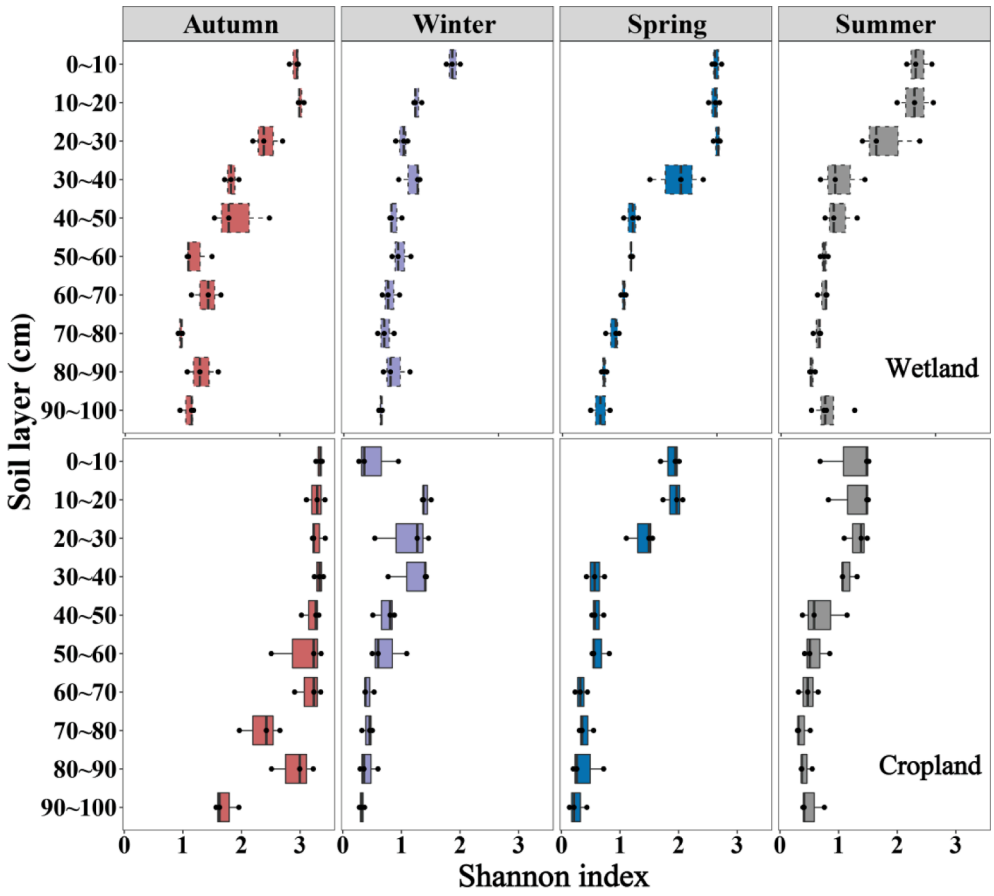

Fig. 1. Shannon diversity is derived from PLFA along soil profiles in wetland and cropland in autumn, winter, spring, and summer.

in both wetland and cropland (Fig. 1). After 23 years of cultivation, the microbial diversity in surface soils reduced from 1.55 to 1 in winter, 2.98 to 1.73 in spring, and 2.43 to 1.27 in summer, respectively, while the effects on microbial diversity in the middle and deep soils were trivial. In the autumn, wetland reclamation promoted the microbial diversity from 1.2 − 3.36 to 2.5–3.42.

The impacts of wetland reclamation on microbial abundances varied along soil depths and over seasons (Fig. 2). The conversion from wetland to cropland significantly decreased the bacterial abundance in the surface soils but increased it in the middle and deep soils (Tables S5 and S7; $p < 0.05$). Along the soil profiles, wetland reclamation continuously decreased fungal abundance (Fig. 2 and Table S5). The strength of

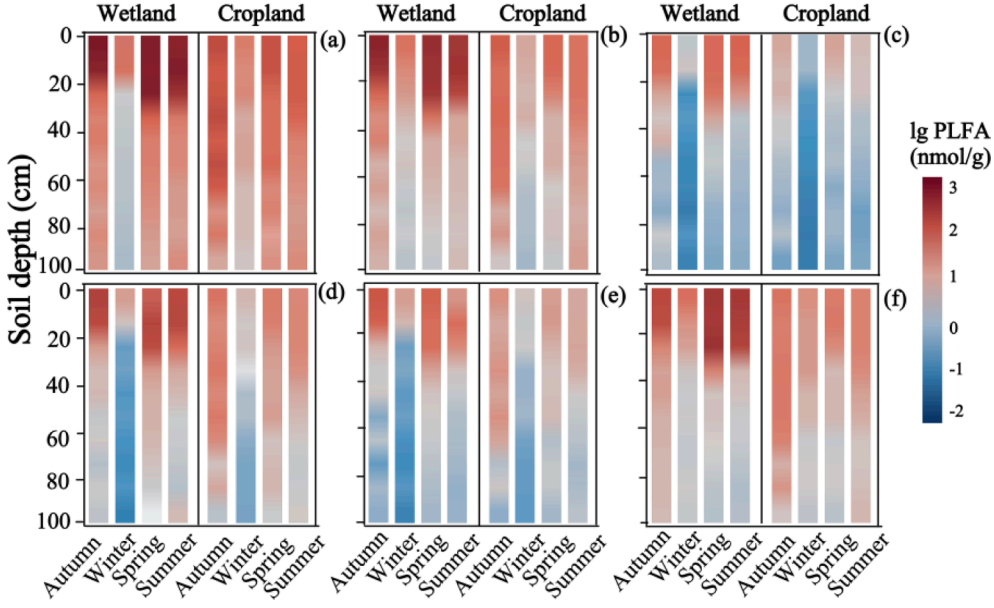

Fig. 2. Microbial biomass of a) total PLFA, b) bacteria, c) fungi, d) Gram-positive bacteria, e) Gram-negative bacteria, f) unspecific bacteria in autumn, winter, spring, and summer for wetland (left) and cropland (right) along soil profiles. All microbial abundance data were log-transformed for presentation.

wetland reclamation impacts on total PLFA varied over the seasons (Fig. 3). Specifically, the total PLFA in the surface soil decreased by approximately 70–90% in the autumn, spring, and summer, whereas exhibited a smaller decline (45–65%) in the winter. The enhancement of bacterial abundance in the middle and deep soils varied over seasons (Table S8); for instance, bacterial abundance increased by 60–367% in the autumn and winter, while increased by 30–137 % in the spring and summer.

There was obvious distinction in the controls of microbial composition between the wetland and cropland (Fig. 4). Most of the distinction were explained by PC1 (86.8%) and PC2 (10.8%), with PC1 functioning as the dominant factor in driving microbial community composition. Compared with the cropland, the wetland samples were more scattered over the four seasons, particularly in the autumn, spring, and summer. PC1 can be clearly explained by the land use types while the PC2 was emphasized by the seasonality.

Although fungal and bacterial abundance, MBC and MBN decreased exponentially with soil depth for both the wetland and cropland, large discrepancies in their vertical profiles were found between cropland and wetland (Fig. 5, Fig S3). It shows that the β values of fungal abundance, bacterial abundance, MBC, and MBN in the wetland were lower than those in the cropland. Meanwhile, the vertical distributions of the microbial abundance and biomass are different; for example, the β values for fungi (0.903) and bacteria (0.905) were lower than that for MBC (0.922) and MBN (0.948) in the wetland. Still, the β values of fungi (0.969), bacteria (0.968), MBC (0.968), and MBN (0.968) were similar in the cropland.

3.2. Edaphic controls on microbial properties

Large discrepancies between soil and microbial properties were found in soil layers of 0 ~ 30 cm and 30 ~ 100 cm (Fig. 6). In the 0 ~ 30 cm soils, the total PLFA, fungi, and bacteria were significantly positively correlated with the TC, TS, MBC, MBN, MBP, and soil temperature and significantly negatively correlated to the land use type ($p < 0.05$). The TC, TN, TS, MBC, MBN, MBP, and MBS had negative relationships with the land use types. The MBC and MBN were positively correlated with the soil temperature, TC, TN, and TS. In the 30 – 100 cm soils, the total PLFA and abundances of fungi and bacteria were significantly positively correlated with the MBC, MBN, and MBP ($p < 0.05$). The fungal abundance was significantly negatively correlated with the land use types and positively associated with TC and TS ($p < 0.05$). The total PLFA and bacterial abundance were significantly positively correlated with land use ($p < 0.05$).

The TS: TM and CF: CP ratios varied between land cover types, across depths, and over seasons (Table 1). In both wetland and cropland, the ratios increased with the soil depth and were the highest in winter. Compared with the wetland, TS: TM in the cropland was higher in surface soils but lower in the middle and deep soils in the autumn, spring, and summer. CF: CP in the cropland was higher than in the wetland along the soil profiles (Table 1).

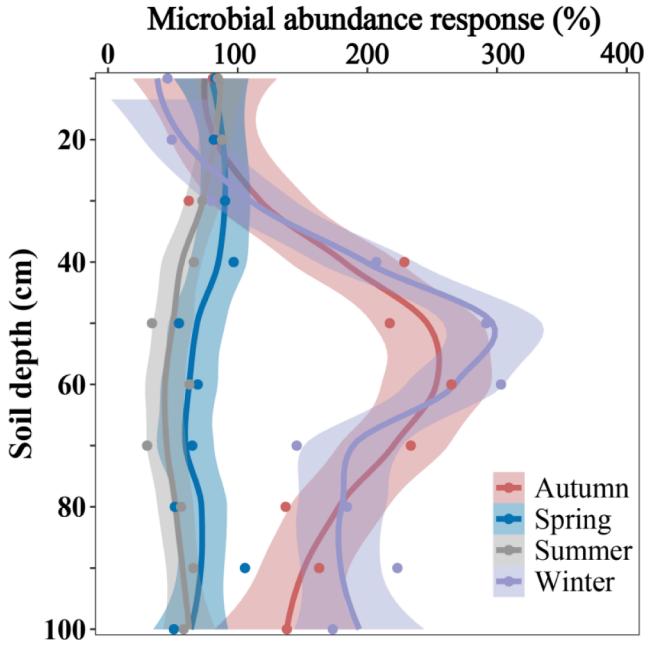

Fig. 3. Responses of PLFA-derived microbial abundance to wetland reclamation and cultivation in autumn, winter, spring, and summer along soil profiles.

3.3. A conceptual diagram for the wetland reclamation impacts on microbial properties

In this study, we found edaphic factors and temperature were the main controlling factors for the microbial properties with the structural equation modeling (Fig. 7). The soil depth significantly influenced the variations of edaphic variables relevant to wetland reclamation and cultivation, such as TC (-0.732) and soil moisture (-0.299). The shifts of edaphic elements (0.152), soil moisture (0.163), and temperature (0.493) together determined the changes in microbial sensitivity to environmental factors. The variations of environmental stress significantly affected the microbial biomass (0.341). In addition, the variations of edaphic elements also contributed to the changes in microbial diversity (0.213) and microbial biomass (0.181). Soil temperature also influenced microbial diversity (-0.211) and microbial composition (-0.164).

Taken together, we presented a conceptual diagram for understanding the wetland reclamation impacts on microbial properties (Fig. 8). The framework highlights the biological mechanisms of wetland reclamation on microbial properties along soil profiles and over seasons. It represents the wetland reclamation impacts on soil properties, such as the decline of soil elements, the increase of edaphic stress for microbial abundance and diversity in surface soils, and the decrease in middle and deep soils. In addition, the framework indicates that microbial abundance and diversity varied among seasons and along soil depth, primarily due to the seasonality and vertical variation of elements availability and temperature.

4. Discussion

4.1. Seasonality of microbial properties along soil profiles

In both the wetland and cropland, the seasonality of microbial diversity, abundance and composition varied along the soil profiles. In the surface soils, the microbial abundance and diversity in the winter were dramatically lower than those in the autumn, spring, and summer (Figs. 1 and 2), which is consistent with the findings of previous studies (Corre et al. 2002; Zifcakova et al. 2017; Wittmann et al. 2004; Wallenstein et al. 2010; Bossio and Scow 1998). The reduction of photosynthate inputs in the form of root exudates and the decline of degradation of macromolecular organic matter in the winter decreased the C availability (Zifcakova et al. 2017), which caused the decline in microbial abundance (Hiroyuki and Tsutomu 1983; Dijkstra and Cheng 2007). Moreover, the soil temperature is an important factor for microbial seasonality because of strong temperature dependences on metabolic activities (Wallenstein et al. 2010; Zifcakova et al. 2017; Yuan et al. 2021a). The seasonality of soil temperature can cause a decline in metabolic activities in winter compared with that in autumn, spring, and summer (Wittmann et al. 2004). However, microbial properties in middle and deep soils remained relatively steady among all seasons (Figs. 1, 2 and 4), resulting from the weak seasonality of environmental factors in the subsurface soils (Tables 1 and S1). Relatively weaker seasonal perturbations on soil substrates and temperatures in the middle

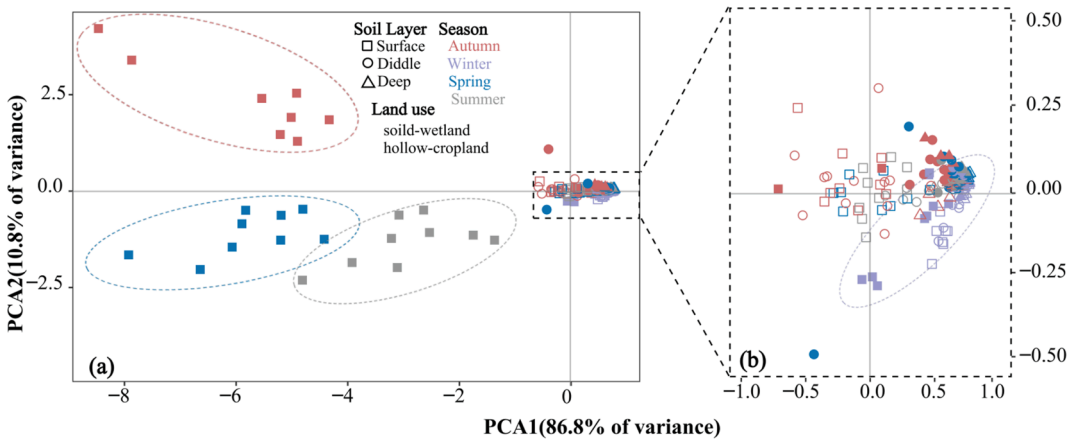

Fig. 4. Principal component analysis of concentrations of microbial groups (fungi, bacteria, and unclassified microbes) for samples from different soil depth (surface, middle, and deep soil), seasons (autumn, winter, spring, and winter), and land use types (wetland and cropland) Surface soils: 0 ~ 10, 10 ~ 20, and 20 ~ 30 cm soil; middle soils: 30 ~ 40, 40 ~ 50, 50 ~ 60, and 60 ~ 70 cm; deep soils: 70 ~ 80, 80 ~ 90, and 90 ~ 100 cm. The dotted circle is used to differentiate the microbial composition in surface soil samples among seasons in the wetland. Red indicates autumn, purple indicates winter, blue indicates spring, and gray indicates summer; the rectangle indicates surface soils, the circle indicates middle soils, the triangle indicates deep soils, the solid indicates wetland, and the hollow indicates cropland. (b) represents a zoom in a portion of the panel (x-axis from −1.0 to 1.0 and y-axis from −0.5 to 0.5). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

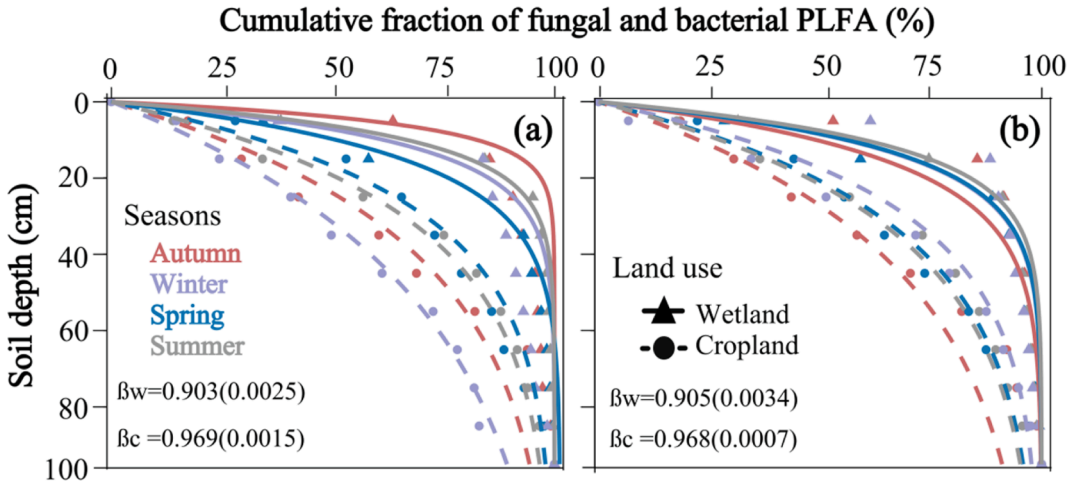

Fig. 5. Vertical distribution of PLFA-derived a) fungal abundance, b) bacterial abundance for four seasons (autumn, winter, spring, and winter) in wetland and cropland. "βc" indicates coefficients of asymptotic equations for the vertical distribution of these microbial properties in cropland; "βw" indicates these coefficients in the wetland.

and deep soils provided a less-varied environment for the microbes, leading to stable microbial properties over seasons. Therefore, the first hypothesis was supported with this study.

4.2. *Wetland cultivation impacts on microbial properties*

Agricultural activities homogenized the microbial properties along soil profiles across seasons (Figs. 4 and S2). Previous studies reported similar patterns in the response of microbial properties to land-use change (Anderson et al., 2017; Zhu et al., 2021). After wetland reclamation, the substantial loss of nutrient content strengthened the edaphic stress (Table 1 and S1) and then significantly decreased the microbial abundance (Fierer et al. 2003). Agricultural perturbations to cropland can promote the transportation of nutrients from the surface soils to middle and deep soils (Zhu et al., 2021), providing a more favorable environment for microorganisms, with lower C and edaphic stress for the microbes in the subsurface soils. The vertical distribution of microbial abundance changes suggested the microbial properties were more homogeneous after perturbations (Fig. 5, Fig S3).

After the wetland reclamation and cultivation, bacterial abundance increased. In contrast, the fungal abundance decreased in the middle and deep soils (Figs. 2 and 8), which indicated that the soil environment under agricultural perturbation might be unfavorable to the fungal community. Tillage activities on soil profiles can physically disturb the fungi. For example, using a plow could tear apart hyphal connections and then dramatically affect the extensive networks of fungal hyphae that ramified and disrupted paths within the mycelia (Young et al. 2000). Alternatively, tillage activities lead to the exposure of organic C to the atmosphere and increase its rapid decomposition (Reicosky 2002; Schlesinger et al. 2000). The massive loss of labile C with wetland reclamation also decreases the ability of fungi to compete in the cropland (de Graaff et al. 2010). In sum, the wetland reclamation and cultivation yielded substantial impacts on microbial composition in soils.

4.3. *Controlling factors on microbial variations*

The strong impacts of edaphic elements on microbial biomass and

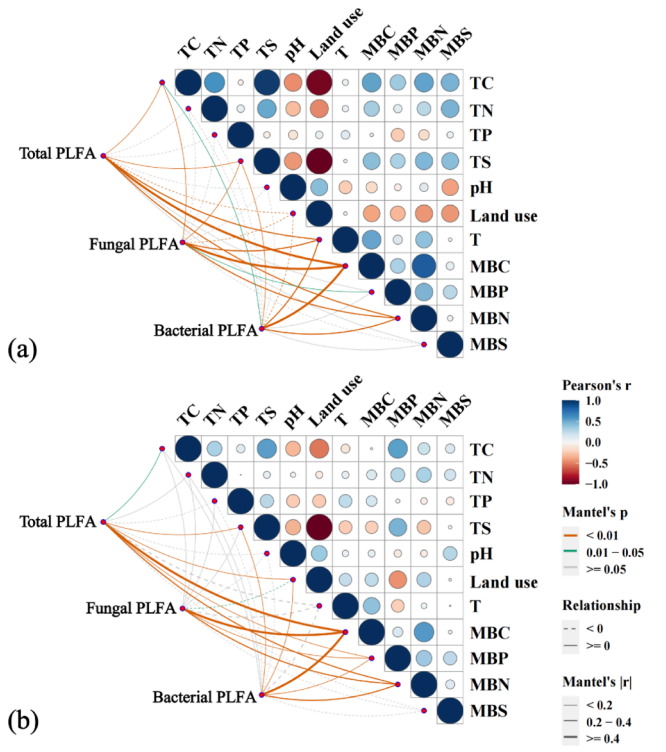

Fig. 6. Mantel's test for the correlations between soil chemical parameters and microbial concentration at a) 0 – 30 cm and b) 30 – 100 cm. The size of circles, i.e., indicates the correlation coefficients between physiochemical soil parameters; small circles indicate weak correlation and vice versa. The correlations between microbial abundance and soil parameters are associated with the line thickness; solid lines indicate a positive correlation and dotted lines indicate a negative correlation; red color indicates significant relations at a significance level of P = 0.01; green color indicates significant relations at a significance level of P = 0.05; gray color indicates insignificant correlations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

diversity variations suggested that the substrates play an essential role in microbial responses to wetland reclamation and cultivation (Fig. 7). As an essential component of nutrient substrates, the soil C available drives microbial diversity and abundance (Korner and Laczko. 1992; Zhang et al. 2021; Fierer et al. 2003). In this study, a larger loss of C led to the more significant reductions in microbial diversity and abundance mainly due to the microbial disappearance owning to microbial adaptation to environmental changes (Anderson et al., 2017; Song et al., 2012).

This study identified the seasonal controls on the microbial response to wetland reclamation and cultivation (Fig. 7), consistent with previous studies on microbial seasonality. Previous studies have reported that soil temperature plays a key role in differentiating microbial abundance and composition (Atkin and Tjoelker 2003; Wallenstein et al. 2010) and regulating microbial respiration and the C use efficiency (Atkin and Tjoelker 2003; Yuan et al. 2021a). Microbial growth rate can escalate with warming (Barcenas-Moreno et al., 2009) because the optimal temperature for microbial growth is typically warmer than the *in situ* soil temperature (Barcenas-Moreno et al., 2009). Therefore, the warmed soil temperature enhanced the microbial biomass and diversity (Fig. 6), enhancing the possibility that some species responded differentially to the changing environments and disturbances. It may also increase the likelihood of microbial redundancy (Naeem and Li 1997; Naeem 1998) and then strengthen the microbial stability. Therefore, it is expected that the microbial communities that inhabit warmer habitats are more resistant to the disturbances caused by environmental changes.

The lowest magnitude of microbial homogeneity in the winter indicated the strong control of soil temperature during wetland conversion. The high homogeneity could explain microbes under low soil temperatures between the surface and subsurface soils in the wetland (Table S5; Fig S2). The freezing temperature in the surface soils, particularly in the cropland, could contribute to the solidification of lipid membranes (Methe et al. 2005) and ice crystals that rupture cell membranes (Methe et al. 2005) both are potentially fatal for microbes. The soil temperature was the lowest in winter. It increased with the soil depth (Fig S4), which contributed to the more considerable temperature limitation of microbial growth rate in the surface soils in the wetland and cropland. To survive freezing temperatures, microbes in the winter soils need to adopt many physiological strategies, such as shifting biochemical pathways and altering membrane lipids to maintain membrane fluidity (Methe

Table 1
Total saturated: total monounsaturated ratios (TS:TM) and cyclopropyl fatty acids: cyclopropyl precursors ratios (CF: CP) in wetland and cropland along soil profiles in autumn, winter, spring, and summer. Values in the table are expressed as mean (SE).

Land use	Soil layer (cm)	Autumn		Winter		Spring		Summer	
		TS:TM	CF: CP	TS:TM	CF: CP	TS:TM	CF: CP	TS:TM	CF: CP
Wetland	0–10	1.26 (0.07)	0.26 (0.06)	2.52 (0.14)	1.75 (0.1)	1.06 (0.02)	0.23 (0.03)	1.47 (0.21)	0.19 (0.01)
	10–20	1.75 (0.02)	0.39 (0.03)	1.56 (0.43)	0.79 (0.32)	1.74 (0.46)	0.28 (0.03)	1.83 (0.06)	0.31 (0.07)
	20–30	1.98 (0.01)	0.59 (0.19)	2.2 (0.12)	0.99 (0.37)	1.31(0.45)	0.25 (0.01)	1.68 (0.04)	0.42 (0.01)
	30–40	2.14 (0.14)	0.99 (0.05)	2.12 (0.29)	0.84 (0.26)	2.57 (0.09)	0.85 (0.04)	2.64 (0.15)	0.85 (0.01)
	40–50	1.83 (0.05)	1.24 (0.18)	1.77 (0.41)	0.83 (0.2)	2.8 (0.05)	0.94 (0.01)	2.57 (0.21)	0.93 (0.02)
	50–60	2.39 (0.06)	1.39 (0.04)	1.72 (0.34)	1.7 (0.13)	2.89 (0.2)	0.93 (0.02)	2.67 (0.16)	1.04 (0.01)
	60–70	2.51 (0.22)	1.53 (0.06)	2.04 (0.37)	1.8 (0.17)	3.02 (0.29)	1.05 (0.01)	2.73 (0.15)	0.93 (0.03)
	70–80	3.05 (0.18)	1.57 (0.11)	1.53 (0.11)	1.89 (0.28)	2.98 (0.15)	0.93 (0.01)	2.63 (0.18)	1.22 (0.14)
	80–90	2.27 (0.04)	1.57 (0.11)	1.59 (0.54)	1.63 (0.08)	2.89 (0.08)	1.13 (0.08)	2.45 (0.02)	1.23 (0.15)
	90–100	2.68 (0.01)	1.5 (0.13)	1.61(0.08)	1.34 (0.24)	2.82 (0.11)	1.1 (0.15)	2.38 (0.06)	1.19 (0.06)
Cropland	0–10	2.13 (0.02)	0.62 (0.08)	2.87 (0.25)	15.64 (0.75)	2.31 (0.26)	0.69 (0.05)	2.33 (0.13)	0.61 (0.01)
	10–20	2.24 (0.14)	0.65 (0.07)	2.55 (0.39)	12.28 (0.69)	2.5 (0.08)	0.71 (0.04)	2.37 (0.19)	0.66 (0.02)
	20–30	2.23 (0.09)	0.59 (0.05)	2.8 (0.64)	26.65 (1.64)	2.57 (0.1)	0.7 (0.05)	2.66 (0.16)	0.7 (0.07)
	30–40	2.46 (0.3)	0.74 (0.08)	2.35 (0.16)	25.64 (0.36)	2.54 (0.2)	0.75 (0.08)	2.62 (0.2)	0.78 (0.08)
	40–50	2.49 (0.23)	0.76 (0.04)	2.25 (0.2)	9.83 (2.19)	2.61 (0.06)	0.71 (0.04)	2.65 (0.25)	0.67 (0.06)
	50–60	2.21 (0.01)	0.84 (0.07)	2.44 (0.2)	4.27 (0.68)	2.69 (0.03)	0.68 (0.05)	2.44 (0.33)	0.7 (0.1)
	60–70	2.24 (0.02)	0.85 (0.01)	2.31 (0.1)	5.65 (0.66)	2.64 (0.08)	0.76 (0.03)	2.53 (0.26)	0.8 (0.02)
	70–80	2.74 (0.03)	0.87 (0.01)	1.85 (0.47)	2.29 (0.47)	2.58 (0.21)	0.71 (0.03)	2.35 (0.39)	0.8 (0.03)
	80–90	2.44 (0.08)	0.86 (0.03)	1.72 (0.62)	1.65 (0.28)	2.72 (0.24)	0.7 (0.1)	2.41 (0.3)	0.85 (0.02)
	90–100	2.55 (0.08)	0.95 (0.02)	1.89 (0.48)	3.82 (0.38)	2.58 (0.37)	0.84 (0.2)	2.27 (0.35)	0.88 (0.04)

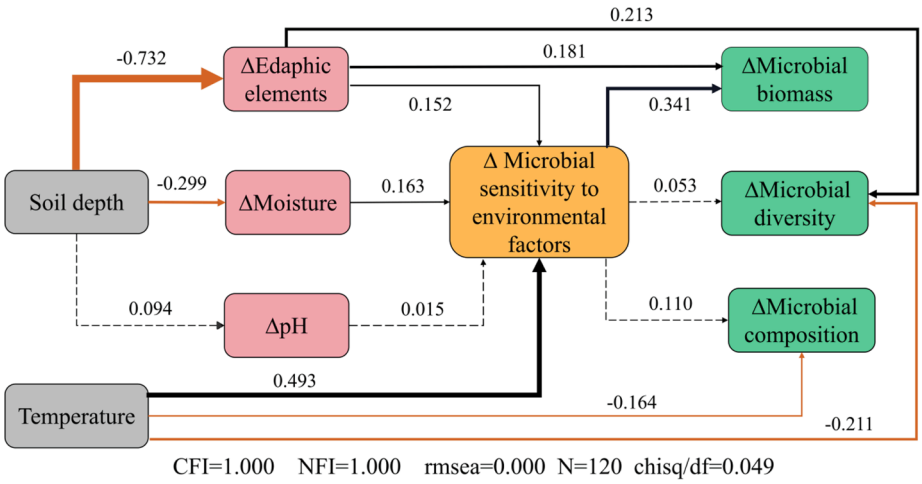

Fig. 7. Structural equation modeling (SEM) of the impacts of environmental changes on the microbial alterations (soil depth, temperature, and variations of edaphic elements (soil TC), microbial sensitivity to environmental factors, microbial diversity (microbial Shannon index), microbial biomass, and microbial composition) black and orange solid arrows represent significant positive and negative effects. Solid lines indicate the relationship was statistically significant ($p < 0.05$). Values associated with the arrows represent standardized coefficients. The results from the best-fitting regression models were comparative fit index (CFI) = 1.000, normed fit index (NFI) = 1.000, Chisqare/df (chisq/df) = 0.038, root mean square error of approximation (RMSEA) = 0.000, and n = 120. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

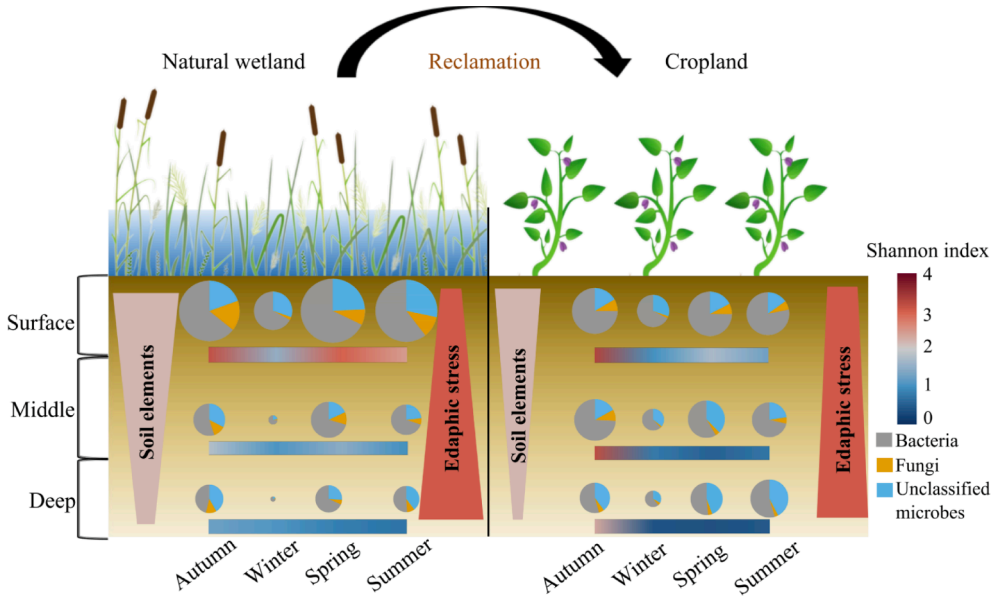

Fig. 8. Conceptual diagram illustrating the impacts of wetland conversion to cropland on microbial properties along soil profiles in four seasons. Wetland reclamation substantially reduced element contents and environmental stress on microbes and then influenced microbial diversity, abundance, and composition of each soil layer.

et al. 2005). However, this ecosystem-level cost of freeze-tolerance is substantial, and a large number of microbial groups disappear during this acclimatization (Methe et al. 2005), which was also supported by the decrease in microbial diversity and microbial abundance in this study (Figs. 1 and 2). In addition, rather than waiting for the freezing stress to occur in winter, microbes could pre-acclimate to the stress (Lennartsson and Ogren 2002). As a result, this physiological process could be conducted above 0℃. Microbes that inhabit the middle and deep soils can also acclimatize under nearly 0℃ in winter soil, enhancing the similarity in microbial abundance and composition between the surface and deep soils.

We found an increase in microbial diversity in the surface soils in the autumn and a relatively higher increase in the middle soils of the autumn and winter. These increases suggested the dramatic influence of seasonal vegetation characteristics on the microbial responses to wetland reclamation and cultivation (Fig. 8). On the one hand, in the autumn, large litter and roots input to the soil as fresh organic C, dramatically changing the microbial properties (Griffiths et al. 1999) and activating the growth of previously dormant microbes. The crop residue could degrade the new substrate or increase the growth rate of active populations with low abundance. These microbial groups grow quickly and specifically metabolize the fresh organic C, and they disappear after their substrates are exhausted (Fontaine et al. 2010). The decrease in the relative abundance of Gram-positive bacteria in the autumn (Fig. S2) could be associated with larger fresh C input since Gram-positive bacteria prefer to utilize recalcitrant soil C as energy sources, and they always have slow growth rates (Wang et al., 2018; Gestel et al. 1993; Farrell et al. 2013). Soybean roots can penetrate up to 68 cm of soil (Gao et al. 2010a), keeping the autumn microbial diversity at a high level in 0 ~ 70 cm soils (Fig. 1). Alternatively, compared with arable crop species, such as soybean, herbs that grow in the wetlands have larger root masses and root length densities, which are more advantageous to the microbial biomass (Haynes and Francis, 1993). Considering that abundant herb roots in the wetland can provide a more hospitable environment for the microbes in growing seasons than cropland soybean without other perturbations, the relatively low microbial increase in the middle and deep soils owing to wetland reclamation was apparent. The fluctuations of environmental factors, including the availability of nutrients, soil temperature, and vegetation, dominated the response of microbial diversity, microbial abundance,

and homogeneity to wetland reclamation in different seasons. Therefore, the second and third hypotheses were also supported in the study.

4.4. Limitations and prospects

This study illustrated the mechanical impacts of wetland reclamation on soil and microbial properties along the soil profiles and over seasons. A few limitations were identified in the current study and will be addressed in future work. First, it was challenging to develop an accurate linkage between the changes in patterns of PLFAs and specific groups of microorganisms when we used the PLFA method to examine the microbial communities in the cropland and wetland. Secondly, the wetland reclamation impacts on microbial properties vary along the soil profiles and over seasons, and they are expected to evolve. Finally, the duration of cultivation may be another key factor for understanding the impacts of wetland reclamation. A few potential topics were also identified for further studies. 1) RNA-based techniques, such as metagenomics of the microbial community and function analysis, will be implemented to develop more accurate linkages between the changes in PLFAs patterns and specific groups of microbes; 2) more measurements of soil microbial properties under a gradient of periods of reclamation will be implemented; and 3) more soil physicochemical parameters, such as soil bulk density, dissolved organic carbon and ammonium, will be measured to understand the microbial mechanisms better. Under the umbrella of microbial macroecology (Xu et al. 2020), the data of soil microbes and their macroecological pattern will also be valuable for further understanding the microbial roles in ecosystem functions across the globe. The data produced in this study can help develop microbial biogeographic patterns and understand their macroecology.

5. Conclusions

This study extracted soil cores to evaluate the impacts of wetland conversion to cropland on microbial properties along the soil profiles over four seasons in northeast China. Wetland reclamation changed microbial properties primarily by altering the soil environmental factors along the soil profiles and across seasons. Soil temperature and vegetation productivity were essential in microbial responses to land conversion over seasons. Although the wetland conversion homogenized the microbial properties along the soil profiles, their magnitudes varied among seasons, associated with soil temperature, nutrient availability, and vegetation productivity. Considerable loss of microbial abundance and functions at the surface soils might accelerate the deterioration of soil quality after wetland reclamation, but their reductions also varied among seasons. This study illustrates the different responses of microbial properties to wetland reclamation in different seasons and confirms the seasonality of microbial processes, which is critically important to better understand the spatial–temporal patterns of soil nutrients cycle during wetland reclamation that have been generally overlooked.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contribution

Xinhao Zhu, Fenghui Yuan and Xiaofeng Xu conceived the idea of the study. Xinhao Zhu, Fenghui Yuan performed the research, analyzed data, and wrote the paper. The remaining authors contributed to refining the ideasa, carrying out additional analyses and finalizing this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2022.106282.

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