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Do climate factors govern soil microbial community composition and biomass at a regional scale?

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Abstract

Soil microbial communities play important role in organic matter decomposition, nutrient cycling and vegetation dynamic. However, little is known about factors driving soil microbial community composition at large scales. The objective of this study was to determine whether climate dominates among environmental factors governing microbial community composition and biomass at a regional scale. Here, we compared soil microbial communities using phospholipid fatty acid method across 7 land use types from 23 locations in North-East China Transect (850 km × 50 km). The results showed that soil water availability and land use changes exhibited the dominant effects on soil microbial community composition and biomass at the regional scale, while climate factors (expressed as a function of large-scale spatial variation) did not show strong relationships with distribution of microbial community composition. Likewise, factors such as spatial structure, soil texture, nutrient availability and vegetation types were not important. Wetter soils had higher contributions of gram-positive bacteria, whereas drier soils had higher contributions of gram-negative bacteria and fungi. Heavily disturbed soils had lower contributions of gram-negative bacteria and fungi than historically disturbed and undisturbed soils. The lowest microbial biomass appeared in the wettest and driest soils. In conclusion, dominant climate factors, commonly known to structure distribution of macroorganisms, were not the most important drivers governing regional pattern of microbial communities because of inclusion of irrigated and managed practices. In comparison, soil water regime and land use types appear to be primary determinants of microbial community composition and biomass.

1 Introduction

Soil microbial communities have important role in organic matter decomposition, nutrient cycling, soil structural formation, and even plant interactions (Wardle et al., 2004; Harris et al., 2009). It is well known that climate factors affect the distributions of plants and animals via ecophysiological constraints at large-scale spatial variation (Whittaker et al., 2001; Jiménez-Valverde et al., 2011). Recently, strong evidence backs the idea that precipitation-energy dynamic exerts a major influence on structuring plant communities along longitudinal and latitudinal gradients (Kreft and Jetz, 2007; Wang et al., 2011). However, the primary driving factor for the regional pattern of soil microbial communities at large spatial scales remains unclear.

At local scales, abiotic factors such as soil water availability (Bossio and Scow, 1998; Drenovsky et al., 2004), soil pH (Pietri and Brookes, 2009), soil depth (Ovreas et al., 1997), nutrient availability (Zhang et al., 2008), seasonality (Bardgett et al., 1999) and plant litter quantity and diversity (Hernandez and Hobbie, 2010) have important effects on soil microbial communities. For instance, water and substrate material additions often alter community composition by selecting for microbial populations that are most competitive in terms of growth rates and ability to absorb water and nutrients (Alden et al., 2001; Ma et al., 2012), and the flooded soils generally had the lowest fungi biomass (Bossio and Scow, 1998; Drenovsky et al., 2004). Plant communities differing in species composition are likely to produce litter and that differ in their chemical composition, which may subsequently influence soil microbial community composition (Zhang et al., 2005a; Eskelinen et al., 2009). As a biotic driver, plants may also exert great effects on soil microbial communities by controlling allocation of belowground photosynthates (Kaiser et al., 2011). The relative importance of these factors at regional scales, however, is still an open question. Available studies showed that soil microbial composition, microbial biomass and diversity vary at large spatial scales (10–3000 km) because of environmental heterogeneity such as climate, vegetation type, soil texture and organic C content (Bird et al., 2002; Šantrucková et al., 2003; Fierer and Jackson, 2006; Martiny et al., 2006; Drenovsky et al., 2010). In one study, soil texture and organic C content exhibited the dominant effects on soil microbial community composition, while climatic effects and vegetation were weaker but still significant along a 1000 km-long transect in Siberia (Šantrucková et al., 2003). In contrast, Bossio et al. (1997) reported that soil microbial community composition was more closely associated with soil type and time than with spatial variation.

Land use varies greatly at regional scales, and land use change is the major reason for spatial heterogeneity. It has been shown that land use changes would lead to great variation in soil microbial community composition in diverse ecosystems (Drenovsky et al., 2010), though their impacts depend on many factors, including the original vegetation that is being replaced, and associated land management practices such as tillage, fallow periods, and related water and nutrient applications, such as irrigation and fertilization (Scanlon et al., 2007). In a recent study, Drenovsky et al. (2010) reported that distinct microbial communities were associated with land use types and disturbance at the regional scale in California. Tillage influences multiple soil physical and chemical properties, disrupts soil fungal hyphae (Evans and Miller, 1990), and alters microbial community composition (Ingram et al., 2008; Drenovsky et al., 2010). Moreover, changes in land use have occurred in temperate area of northeast China as a result of expansion of farmlands and grazed rangelands at the expense of natural habitats, however, little is known about soil microbial community composition to land use changes at large spatial scales.

A better understanding of the effects of environmental factors (e.g. habitat, land management, spatial structure) on soil microbial community composition and biomass could help to reduce uncertainties in our predictions of the geographic distribution of microbial communities. For this purpose, 451 samples from 23 locations across 7 land use types (i.e. rangeland, artificial grassland, grazed rangeland, farmland, returned cropland, woodland, rice field) were selected to compare soil microbial communities at a regional scale in North-East China Transect. We hypothesize that climate, especially precipitation variation, is the primary driver to affect soil microbial community composition and biomass at the regional extent, following the finding that precipitation is the dominant driver for variation of plant community composition in this transect (Wang et al., 2003).

2 Materials and methods

2.1 Study locations

The field study was conducted on a large spatial scale (43°12′–44°36′ N; 114°34′–124°18′ E) across Jilin province and Inner Mongolia (about 850 km from east to west, and 50 km from north to south) with 23 locations in North-East China Transect (NECT) (Table 1, Fig. 1). The NECT was identified as a core project of International Geosphere-Biosphere Programme (IGBP) which represents an array of regional-scale gradients on all continents that vary in major environmental variables (Koch et al., 1995). This area has a continental monsoon climate, with large seasonal temperature and precipitation gradients. Long-term (1950–2000) mean annual temperature, precipitation and radiative dry index at this large spatial scale range from approximately 1.3–6.8 °C, 237–472 mm and 0.91–1.44, respectively. The elevation gradients range from 140 to 1309 m (http://www.worldclim.com; Zhang et al., 1997; Table A1). Mean soil total C, N and C: N varied 3.3-fold, 2.4-fold and 2.7-fold across the region. Overall, there were 7.4-fold and 2.8-fold differences in soil water content and water holding capacity, whereas soil origin and pH differed slightly (Table A1).

Spatial climatic variability, especially precipitation, is one of the most notable features of the transect. Due to the steep decrease in precipitation from the east (Jilin province) to the west (Inner Mongolia), vegetation vary gradually from moist meadows in the east to typical steppes and desert steppes in the west with farmlands, returned croplands and woodlands spread evenly across the gradient (Wang et al., 2003, 2011; Table A1). All farmlands were irrigated only several times (2–3 times) during the growing season, and rice field was flood-irrigated. The large spatial region have remarkable variations in climate, land use types and vegetation types, which make it an ideal region for studying the primary factor that driving soil microbial community composition and biomass. A detailed description of land use types, vegetation types, soil properties can be found in Tables 1 and A1, Zhang et al. (1997) and Ni and Zhang (2000).

2.2 Soil samplings

451 soil samples from 23 locations including 7 land use types were collected along the NECT in 12–18 July 2012. 6–16 soil core samples were collected randomly per site (100 m × 100 m) for determination of soil microbial communities (Table 1).

The samples were taken with a cylindrical soil sampler (5 cm inner diameter, 15 cm length) for the 0–15 cm layer, and then immediately preserved at 4 °C in a cooler for transport to the laboratory within one week of collection. The fresh samples were processed using a 2 mm sieve and manually cleaned of any visible plant tissues. Two subsamples of each sample were obtained; one was air dried for routine soil analyses and the other was stored at −70 °C, for phospholipid fatty acids analysis.

2.3 Soil microbial community analysis

Phospholipid fatty acids (PLFAs) were extracted and quantified from 8.0 g (dry weight equivalent) soils using a procedure described by Bossio and Scow (1998). The separation and identification of extracted PLFAs were carried out according to the standard protocol of the Sherlock Microbial Identification System $V_{4.5}$ (MIDI) and a Gas Chromatograph (Agilent 6850, USA). "A : BωC" represents the number of carbons in the compound: the number of double bonds in the carbon chain, followed by double bond location from the methyl (ω) end of the molecule (Bossio and Scow, 1998). Cis and trans conformations are indicated by the suffixes c and t. The prefixes a and i indicate anteiso and iso branching; 10Me specifies a methyl group on the 10th carbon from the carboxyl end of the molecule; OH indicates a hydroxyl group; and cy indicates cyclopropane fatty acids. In addition, the fatty acids "sum" indicates imperfect peak separation occurs, and refers two or more fatty acids having the same retention time (Drenovsky et al., 2004).

Thirty-one fatty acids were included in the analyses. (1) branched fatty acids indicative of gram-positive bacteria: a13:0, i14:0, i15:0, i16:0, i17:0 and a17:0, (2) monounsaturated fatty acids indicative of gram-negative bacteria: 16:1ω7c, 17:1ω8c, 18:1ω5c, 18:1ω9t, 17:0cy and 19:0cy (Frostegård et al., 1993, 1996), (3) saturated fatty acid (common in soil microorganism): 14:0, 15:0, 16:0, 17:0, 18:0 and 20:0, (4) two fatty acids (18:2ω6c, 18:1ω9c) were chosen to represent the fungi (Frostegård et al., 2011), (5) actinomycetes was represented by 10Me 17:0 fatty acid. The fatty acids 14:2ω6c and 14:1ω8c were unique in three samples which were excluded in the data set. The ratio of 17:0cy (17cy) to 16:1ω7c (precursor) was used to as an indicator of physiological stress (Knivett and Cullen, 1965). The viable microbial biomass was calculated by summing concentration of all fatty acids detected in each soil samples (White et al., 1979). Total percentages of fatty acid identified for each microbial group was calculated to represent their relative contributions to the total microbial biomass. The fungal: bacterial fatty acid (gram-positive + gram-negative bacteria) was also included in the data analysis (Frostegård et al., 1996).

2.4 Soil property analyses

Soil inorganic N (NH_4^+-N + NO_3^--N) was extracted with 2M KCl solution, and the extractant was determined using a flow injection autoanalyzer (FIAstar 5000, Denmark). Soil pH was measured at a soil : water ratio of 1 : 2.5 with a pH electrode (PHS 29, China). Soil total C and N content were measured by elemental analyzer (Elemetaranalysator vario Max CN, Germany). Soil texture was determined by the optical size analyzer (Mastersizer, 2000, England). Gravimetric soil water content was measured by oven-drying samples at 105 °C for 24 h. Soil water holding capacity was measured by Wilcox method (Wilcox, 1962).

2.5 Statistical analyses

Unconstrained ordination–correspondence analysis (CA) was used to compare soil microbial communities among samples ($n = 451$) using the Canoco for Windows 4.5 package (Ithaca, NY, USA). CA is an indirect gradient analysis method which can provide the basic overview of soil samples, and maximize the correlation between fatty acids and samples (Lepš and Smilauer, 2003). Constrained ordination–canonical correspondence analysis (CCA) was used to represent the relationships among environmental factors (habitat, land management, spatial structure), sample patterns, and fatty acids distributions (Lepš and Smilauer, 2003). Qualitative factors were coded for the program using a set of "dummy factors". That is, if a sample has a particular value of the factor, then the corresponding dummy factor has the value 1.0, and the other dummy factors have a value of 0.0 for the same sample.

In order to separate the effects of environmental factors on microbial communities, the variation partitioning procedure with CCA were used in the analysis (Borcard et al., 1992). The environmental factors were divided into three groups: (1) habitat (mean annual temperature, mean annual precipitation, radiative dry index, elevation, soil texture, pH class, soil N availability, soil C and N content, water holding capacity), (2) land management (tillage, grazing, historically tillage), (3) spatial structure (x, y, xy, x^2, y^2, x^2y, xy^2, x^3, y^3). The third group consisted of nine terms, in which latitudinal (x) and longitudinal (y) coordinate were used to calculate a cubic trend surface (Legendre, 1990). The variation partitioning procedure decomposed the total variability into eight parts: individual effect of habitat (X_1), land management (X_2), spatial structure (X_3), combined effects of habitat and land management (X_4), combined effects of land management and spatial structure (X_5), combined effects of habitat and spatial structure (X_6), combined effects of the three groups of environmental factors (X_7), and residual variation (X_8). A complete explanation of these partitioning analyses can be found in Lepš and Smilauer (2003).

Stepwise multiple linear analyses were used to determine the relationships of soil microbial biomass or contribution of each microbial group with environmental factors. Differences among the sites in soil microbial biomass and contribution of each microbial group were tested using One-way ANOVAs. Data management and statistical analyses were performed using SPSS 17.0 software (SPSS, Chicago, IL, USA).

3 Results

3.1 Variation of soil microbial communities

The first axis of CA ordination, which explained 27.5 % of the variation in microbial community composition, mainly reflected soil water gradients and management intensity (Fig. 2a and b). Wetter soils (e.g. rice field, moisture rangeland) and heavily disturbed soils (e.g. farmland) with more branched fatty acids (gram-positive bacteria: a13:0, i14:0, i15:0, i16:0, i17:0) and saturated fatty acids (14:0, 15:0, 16:0, 17:0, 18:0, 20:0) were positioned along the right side of the first axis. Drier soils, lightly and historically disturbed soils (e.g. dry rangeland, grazed rangeland, returned cropland) with more fungi (18:2ω6c, 18:1ω9c) and monounsaturated fatty acids (gram-negative bacteria: 16:1ω7c, 16:1ω9c, 17:1ω8c, 18:1ω5c, 18:1ω9t) were plotted along the left side of the first axis.

The second axis, which described 20 % of the variation of the composition, mainly associated with management practices and spatial variation (expressed as underlying effects of soil properties). In heavily disturbed habitat, soils from flood-irrigated rice field had different microbial communities with soils from farmland, which were separated along the second axis (Fig. 2a). In addition, microbial community composition varied greatly among different locations within the same land use type (e.g. woodland, farmland, returned cropland), which can be observed along the second CA axis (Fig. 2a).

3.2 Relationship between microbial communities and environmental factors

Similar to the CA ordination, soil microbial community composition across 7 land use types at the regional scale was distinguished by environmental factors with the CCA ordination (Fig. 3a and b). The first axis, which was mainly associated with water regime (i.e. soil water availability) and water holding capacity, explained 22 % of the variation in microbial community composition. The second axis described 15.2 % of the variation, which were primarily related to management intensity (tillage > historically tillage or grazing). Climate factors (mean annual precipitation and temperature, radiative dry index, elevation) did not show strong relationships with distribution of microbial communities. Factors such as soil texture (sandy loam), soil inorganic N content and pH plotted near the origin, thus would not be the major drivers of microbial community composition (Fig. 3b).

3.3 Variation partitioning

Forward selection of the three groups of environmental factors with CCA suggested that the soil microbial community composition was significantly related to the habitat (X_1) (mean annual precipitation and temperature, radiative dry index, elevation, soil texture, pH, soil nutrient content, water holding capacity) and land management (X_2) (tillage, grazing, historically tillage). The variation partitioning procedure showed that total explained variation of microbial community composition was 64.6 % ($X_1 + X_2 + X_3 + X_4 + X_5 + X_6 + X_7$) and undetermined variation of it was 35.4 % (X_8) (Fig. 4). The largest unique fraction in the explained variation was the effect of habitat (X_1: 27 %), which had a strong overlap with land management (X_4: 11 %). In addition, the land management effect was also considerable (X_2: 12.2 %), whereas the unique effect of spatial structure (X_3: 2.8 %) was very small and statistically not significant.

3.4 Soil microbial biomass and contributions of microbial group

The soil microbial biomass (i.e. total PLFAs) or the contribution of each microbial group in the same land use type, such as rangeland, farmland or woodland, varied significantly at different sample locations along the transect ($P < 0.05$, One-way ANOVAs). The total PLFAs varied 2.4-fold across all the land use types (Fig. 5a). The highest value appeared in one of the rangelands (ca 35 nmol g^{-1}), and the lowest value appeared in rice field (ca 16 nmol g^{-1}). The total PLFAs in artificial grassland, grazed rangeland, farmland and returned cropland had intermediate values.

Relative contribution of branched, monounsaturated, actinomycetes, saturated and fungi PLFAs to total PLFAs were represented by the total percentage of their PLFAs identified in soils (Fig. 5b–f). Contribution of each microbial group across 7 land use types varied significantly, except that of actinomycetes. The percentages of monounsaturated and fungi PLFAs tended to decreases, and those of branched and saturated PLFAs displayed increase trends in heavily disturbed and wetter sites. Instead, undisturbed and drier soils had higher percentages of monounsaturated and fungi PLFAs, and lower percentages of branched PLFAs.

One of the rangelands (i.e. desert steppe) had the lowest percentage of branched PLFAs (ca 13 %), and rice field had the highest value (ca 25 %) (Fig. 5b). On the contrary, the lowest percentage of monounsaturated PLFAs were in one of farmlands (ca 10.2 %), and the highest value was in one of rangelands (ca 29.5 %) (Fig. 5c). The percentages of saturated PLFAs in rice fields (ca 23 %) were higher than other land use types. In addition, one of the rangelands (i.e. desert steppe) had the highest fungal contribution (ca 13 %), having 3-fold greater than rice fields, which had the lowest contribution (ca 4.5 %) (Fig. 5f). Similar to the variation of fungi, the highest fungal: bacterial PLFAs (ca 0.35) were appeared in one of the rangelands, and the lowest value occurred in rice field (ca 0.15) (Fig. 5g). Surprisingly, 17cy:precursor (used as an indicator of the anaerobic stress) across 7 land use types fluctuated disorderly at this regional scale (Fig. 5h).

Stepwise multiple regression analysis demonstrated that 32 % of the variation in total microbial biomass could be explained by soil water content, soil C content and radiative dry index. Soil water content alone contributed to 57, 52, 49 and 57 % of the variation in the contributions of branched, monounsaturated, saturated and fungal PLFAs, respectively. In this region, radiative dry index, soil water content, water holding capacity together accounted for 58 % of the variation in fungal: bacterial PLFAs (Table 2).

4 Discussion

Inconsistent with the hypothesis, soil water availability (associated natural and managed water inputs) and land management were the primary determinants of regional pattern of soil microbial community composition. However, climate factors (mean annual precipitation and temperature, radiative dry index, elevation) did not show strong relationships with distribution of microbial communities. Other factors, such as spatial structure, soil texture, nutrient availability and vegetation types were not major drivers (Fig. 3, Table 2).

In general, soil water availability was positively related to the contribution of gram-positive bacteria, and was negatively related to gram-negative bacteria and fungi across 7 land use types at the regional scale (Fig. 5; Table 2). The stress of drought likely facilitates fungi to survive better, because soil fungi rely on more aerobic conditions (Šantrucková et al., 2003; Zhang et al., 2005a) and are more tolerant to drought due to their filamentous nature (Holland and Coleman, 1987). The aerobic filamentous fungi have variable hyphal networks that can relocate water and nutrient resource by cytoplasm translocation (Klein and Paschke, 2004). Instead, the predominance of bacteria over fungi indicates adaptation of the soil microbial communities to high water potential and limited aeration of the soils (Šantrucková et al., 2003; Drenovsky et al., 2004). These findings were also supported by the previous observations (Bossio and Scow, 1998; Rinklebe and Langer, 2006; Entry et al., 2008; Drenovsky et al., 2004, 2010).

It has been proposed that the ratio of cyclopropane fatty acids to its precursor can be used to indicate the levels of anaerobic and nutritional stress (Law et al., 1963; Knivett and Cullen, 1965). For instance, Knivett and Cullen (1965) and Drenovsky et al. (2010) have reported that cyclopropane fatty acid:precursor (17cy/16:1ω7c; 19cy/18:1ω7c) were significant high under conditions of low O_2 concentration and high temperature. However, whether cyclopropane fatty acid is representative of aerobic conditions is debatable. Bossio and Scow (1998) reported that the cyclopropane fatty acids were insensitive to water availability across a large-scale precipitation gradient in California. Similarly, our result also showed that the 17cy:precursor responded to high water availability modestly (Fig. 5h), whereas we do not know for sure what limits the cyclopropane formation. This insensitivity to anaerobic conditions in the soils contrasts with its widespread use an anaerobic marker. These findings suggest that cyclopropane fatty acids to its precursor are not generally useful as taxonomic indicators of respiratory type at large spatial scales.

We found that the heavily disturbed soils had higher contributions of gram-positive bacteria, and had lower contributions of fungi (Fig. 2b). The ability of gram-positive bacteria to sporulate may allow them with stand tillage or other anthropogenic disturbance. In contrast, fungi are sensitive to disturbance and their hyphae density would decrease significantly in response to tillage (Drenovsky et al., 2010). Continuously farmed agriculture is widely occurring in various biomes across the world. Repeated tillage heavily disturbs soil physical properties, and decreases soil bulk density and water retaining capacity (Six et al., 2004; Osunbitan et al., 2005; Bescansa et al., 2006). This frequent disturbance in soil properties during tillage (and associated fertilization) could rapidly alter microbial community composition due to different competitive ability of specific microbial groups. The groups with the capacity of rapid adaptation to the frequently changing soil environment (e.g. bacteria) could take advantage of new resources in disturbed habitats (Andrews and Harris, 1986). Sustainable tillage contributes to the decreases of soil fungi and the increases of gram-positive bacteria at both local and regional scales (Galvez et al., 2001; Zhang et al., 2005a).

Given the strong effects of heavy soil disturbance on soil microbial community, it is interesting to find that microbial community composition in lightly and historically disturbed soils (i.e. grazed rangelands, returned croplands) were similar to those in undisturbed soils. As the disturbance intensity decreased, microbial biomass increased, probably because more time and resources were available for specific microbial groups which have slower growth rate (e.g. fungi) (Zhang et al., 2005b).

These results were in line with a few studies (Bardgett and McAlister, 1999; Ingram et al., 2008). As Ingram et al. (2008) proposed, light grazing showed no effect on soil C content and slightly increased gram-negative bacteria and fungi proportions. These results indicate land disturbance with moderate intensity would have neutral effects on soil microbial community composition.

Although a few reports showed that vegetation types can influence the characteristics of the soil microbial communities through providing suitable habitats and food sources at landscape and region scales (McArthur et al., 1988; Kourtev et al., 2003; Šantrucková et al., 2003; Han et al., 2007), our findings of microbial community composition were more related to the soil environment (e.g. water availability) than natural vegetation types at the regional extent. In our study, soils were sampled in different vegetation types, but the microbial community composition were very similar at the same geographical location in natural habitats (e.g. meadow vs. wood, data not shown) (Fig. 5). Similar trends were observed in heavily disturbed habitat, the microbial community composition were depended on land disturbance intensity and practices rather than agricultural vegetation types, because the farmland soils (e.g. corn, peanut, mung bean, red bean) in the same location clustered together in CCA ordination despite the different vegetation types that they represented (Figs. 2, 3 and 5). Likewise, Drenovsky et al. (2010) also reported that microbial community composition was more strongly influenced by disturbance than by agricultural vegetation types in California.

The results showed that habitat and land management factors triggered complex interactive effects on soil microbial community composition at the regional scale in northeastern China, as the value of shared variance fraction was 11 % without considering the variation explained by all three components (Fig. 4). This was similar to the findings of Drenovsky et al. (2010) that environmental factors caused significantly interactions on microbial community composition at large spatial and temporal scales in California. The significant shared effects in our study could be attributed to the strong effects of land management on soil properties that then affect microbial communities.

The findings suggest that management practices could have larger effects on microbial community composition and biomass than habitat factors at large spatial scales.

In conclusion, soil water availability and land use changes were the most important factors driving microbial community composition and biomass at the regional scale in northeastern China. Soil water availability in this study was determined not only by natural precipitation, but also by managed inputs, thus the effect of precipitation was weaker but still significant. In addition, factors such as spatial structure, soil texture, soil nutrient content and vegetation types did not have significant relationships with microbial community composition. These findings will improve predictions of the ecological processes and consequences of ecosystems under global changes.

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Table 1. Sample locations (1–23), coordinates of the sample location, land use types, vegetation types and number of replicates (*n*).

Location	No.	Coordinate	Land use type	Vegetation type	*n*
Baogedawula	1	43°56′ N; 114°34′ E	Rangeland	Desert steppe	8
Dabuxiletu	2	43°55′ N; 115°44′ E	Rangeland	Desert steppe	8
	2		Grazed rangeland	Desert steppe	8
Aqiwula	3	43°33′ N; 116°40′ E	Rangeland	Steppe	10
	3		Woodland	Wood and shrub	8
Dalainuori	4	43°16′ N; 117°09′ E	Rangeland	Steppe	8
Sanyi	5	43°12′ N; 117°18′ E	Woodland	Wood and shrub	8
Xinchengzi	6	43°27′ N; 118°04′ E	Rangeland	Steppe	14
	6		Returned cropland	Alfalfa	8
Xinfuzhilu	7	43°43′ N; 119°04′ E	Grazed rangeland	Steppe (site 1)	4
	7			Steppe (site 2)	4
Tianshan	8	43°50′ N; 119°55′ E	Rangeland	Steppe	8
	8		Returned cropland	Almond	16
Tianshan	9	43°50′ N; 120°15′ E	Rangeland	Steppe	9
	9		Returned cropland	Almond	9
Shaogen	10	43°38′ N; 120°47′ E	Rangeland	Steppe (site 1)	8
	10			Steppe (site 2)	8
	10		Farmland	Corn	8
Molimiao	11	43°34′ N; 121°55′ E	Rangeland	Steppe (site 1)	8
	11			Steppe (site 2)	8
	11		Farmland	Corn	8
Yuxin	12	43°34′ N; 121°59′ E	Rice field	Rice	14
Baixingtu	13	43°52′ N; 122°41′ E	Woodland	Wood and shrub	8
Baolongshan	14	43°56′ N; 122°42′ E	Rangeland	Meadow (site 1)	7
	14			Meadow (site 2)	6
	14		Farmland	Corn	8
Jiamatu	15	44°01′ N; 122°56′ E	Rangeland	Meadow (site 1)	8
	15			Meadow (site 2)	8
	15		Farmland	Corn	8
	15			Red bean	7
Taipingchuan	16	44°21′ N; 123°14′ E	Rangeland	Meadow	9
	16		Rice field	Rice	9
Yaojingzinan	17	44°21′ N; 123°14′ E	Woodland	Wood and shrub (site 1)	11
	17		Woodland	Wood and shrub (site 2)	10
	17		Farmland	Peanut	8
Yaojingzi	18	44°34′ N; 123°29′ E	Rangeland	Meadow (site 1)	8
	18			Meadow (site 2)	7
	18		Farmland	Peanut	8
	18			Mung bean	8
	18			Corn	8
Yaojingzi	19	44°35′ N; 123°30′ E	Rangeland	Meadow	14
Yaojingzi	20	44°34′ N; 123°31′ E	Artificial grassland	Meadow (site 1)	7
	20			Meadow (site 2)	8
	20		Farmland	Corn	8
Wulanaodu	21	44°36′ N; 123°48′ E	Rangeland	Meadow (site 1)	8
	21			Meadow (site 2)	8
	21		Farmland	Corn	7
	21		Woodland	Wood and shrub	9
Chaganhua	22	44°35′ N; 124°16′ E	Rangeland	Meadow (site 1)	8
Wulantuga	22 23	44°28′ N; 124°18′ E	Rangeland	Meadow (site 2) Meadow	8
					8
	23		Farmland	Corn	6
	23			Peanut	6
	23		Woodland	Wood and shrub	8
				Total	451

Table 2. Results of stepwise multiple regression analyses. Dependent variables: soil water content (SWC, %), soil total carbon and nitrogen content (C, N, %), ratio of soil C to N (C : N), pH, mean annual precipitation (MAP), radiative dry index (RDI) and soil water holding capacity (WHC); Independent variable: soil total PLFAs (i.e. microbial biomass, TPLFAs, nmol g^{-1}), percentages of branched PLFAs (gram-positive bacteria) (BP, %), monounsaturated PLFAs (gram-negative bacteria) (MP, %), saturated PLFAs (common in microorganism) (SP, %), fungal PLFAs (F, %), bacterial PLFAs (B, %) and fungal : bacterial PLFAs (F : B). Negative values of parameter estimate refer negative relationships between the examined dependent variables and the independent variables.

	Variable entered	Parameter estimate	Partial r^2	Probability
TPLFAs	SWC	0.054	0.11	0.000
	C	0.805	0.11	0.000
	RDI	1.791	0.10	0.000
	pH	1.262	0.06	0.002
BP	SWC	0.318	0.57	0.000
MP	MAP	−0.053	0.52	0.000
	SWC	−0.191	0.09	0.000
	C : N	0.799	0.05	0.000
SP	SWC	0.191	0.49	0.000
	RDI	−7.451	0.09	0.000
F	RDI	7.708	0.57	0.000
	SWC	0.073	0.06	0.000
B	MAP	−0.035	0.20	0.000
	C	1.803	0.07	0.000
F : B	RDI	0.205	0.42	0.000
	SWC	−0.007	0.11	0.000
	WHC	0.006	0.05	0.000

Table A1. Sample locations (1–23, see Fig. 1), land use types, land management practices, vegetation types, climatic indices and soil properties. MAP, mean annual precipitation (mm); MAT, mean annual temperature (°C); RDI, radiative dry index; ELE, elevation (m); TC, soil total C (%); TN, soil total N (%); SWC, soil water content (%); WHC, water holding capacity; IN, soil inorganic N content (mg kg^{-1}); SL, sandy loam; LS, loamy sand.

Location	No.	Land use type	Management practices	Vegetation type	MAP	MAT	RDI	ELE	pH	Soil texture	C	N	C : N	SWC	WHC	IN
Baogedawula	1	Rangeland	Undisturbed	Desert steppe	237	1.7	1.44	1092	7.7	LS	0.67	0.12	5.32	3	12	2.05
Dabuxiletu	2	Rangeland	Undisturbed	Desert steppe	276	1.4	1.37	1158	7.8	LS	0.79	0.1	7.94	5	15	2.47
	2	Grazed rangeland	Grazed	Desert steppe	276	1.4	1.37	1158	7.9	LS	0.81	0.11	7.31	5	17	3.30
Aqiwula	3	Rangeland	Undisturbed	Steppe	340	1.3	1.33	1239	8.8	SL	1.45	0.15	9.78	7	17	3.46
	3	Woodland	Undisturbed	Wood and shrub	340	1.3	1.33	1239	7.8	SL	0.7	0.15	4.48	9	20	3.32
Dalainuori	4	Rangeland	Undisturbed	Steppe	385	1.3	1.21	1309	8.1	LS	0.84	0.14	7.67	8	18	3.77
Sanyi	5	Woodland	Undisturbed	Wood and shrub	380	2.3	1.21	1173	8	SL	1.11	0.14	7.94	9	22	7.70
Xinchengzi	6	Rangeland	Undisturbed	Steppe	397	3.5	1.23	919	7.7	LS	1.52	0.15	10.07	10	22	4.08
	6	Returned cropland	Historically tilled	Alfalfa	397	3.5	1.23	919	7.7	SL	0.9	0.1	9.96	9	23	7.79
Xinfuzhilu	7	Grazed rangeland	Grazed	Steppe (site 1)	386	5.8	1.18	735	8.4	LS	0.97	0.11	8.95	8	25	5.87
	7		Grazed	Steppe (site 2)	386	5.8	1.18	735	8.3	LS	0.99	0.12	8.05	8	25	4.84
Tianshan	8	Rangeland	Undisturbed	Steppe	386	5.8	1.18	513	8.3	LS	1.66	0.19	8.48	8	23	6.14
	8	Returned cropland	Historically tilled	Almond	386	5.8	1.18	513	8.2	SL	0.9	0.1	8.71	10	25	13.08
Tianshan	9	Rangeland	Undisturbed	Steppe	388	5.8	1.18	413	8.2	LS	1.63	0.19	8.36	9	22	5.24
	9	Returned cropland	Historically tilled	Almond	388	5.8	1.18	413	8.2	SL	1.81	0.17	10.78	10	24	7.34
Shaogen	10	Rangeland	Undisturbed	Steppe (site 1)	385	6.8	1.12	270	8	LS	0.85	0.11	7.66	12	25	5.14
	10		Undisturbed	Steppe (site 2)	385	6.8	1.12	270	8.2	LS	1	0.11	9.36	11	25	4.58
	10	Farmland	Tilled	Corn	385	6.8	1.12	270	8.6	LS	0.9	0.11	8.08	11	24	20.80
Molimiao	11	Rangeland	Undisturbed	Steppe (site 1)	399	6.3	1.05	179	8.4	SL	1.05	0.12	8.85	12	25	7.52
	11		Undisturbed	Steppe (site 2)	399	6.3	1.05	179	8.4	SL	1.1	0.15	7.30	13	25	6.65
	11	Farmland	Tilled	Corn	399	6.3	1.05	179	8.4	SL	1	0.11	9.13	10	25	6.34
Yuxin	12	Rice field	Periodically flooded	Rice	397	6.3	1.02	211	7.8	SL	1.23	0.15	8.23	32	32	5.23
Baixingtu	13	Woodland	Undisturbed	Wood and shrub	414	6	1.02	159	7.7	SL	0.97	0.12	8.08	13	28	8.85
Baolongshan	14	Rangeland	Undisturbed	Meadow (site 1)	415	6	1	156	7.9	SL	1.3	0.13	9.02	13	26	8.45
	14		Undisturbed	Meadow (site 2)	415	6	1	156	7.8	SL	1.34	0.15	8.43	13	27	7.62
	14	Farmland	Tilled	Corn	415	6	1	156	7.7	SL	1.3	0.11	11.92	12	27	6.24
Jiamatu	15	Rangeland	Undisturbed	Meadow (site 1)	422	6	1	149	8.2	SL	1.73	0.17	10.20	14	27	6.08
	15		Undisturbed	Meadow (site 2)	422	6	1	149	8.3	SL	1.77	0.18	10.07	13	28	6.22
	15	Farmland	Tilled	Corn	422	6	1	149	8.2	SL	1.22	0.17	7.19	11	25	10.34
	15		Tilled	Red bean	422	6	1	149	8.4	SL	1	0.17	5.56	10	25	18.35
Taipingchuan	16	Rangeland	Undisturbed	Meadow	428	5.6	0.97	150	8.6	LS	1.02	0.13	8.07	18	31	7.37
	16	Rice field	Periodically flooded	Rice	428	5.6	0.97	150	8.3	SL	1.18	0.12	9.83	35	35	8.93
Yaojingzinan	17	Woodland	Undisturbed	Wood and shrub (site 1)	435	5.4	0.97	150	7.9	SL	0.98	0.13	7.27	14	29	5.78
	17	Woodland	Undisturbed	Wood and shrub (site 2)	435	5.4	0.97	150	7.9	SL	1.16	0.16	7.27	13	28	5.78
	17	Farmland	Tilled	Peanut	435	5.4	0.97	150	7.5	LS	0.9	0.15	5.97	10	30	3.23
Yaojingzi	18	Rangeland	Undisturbed	Meadow (site 1)	435	5.4	0.97	159	7.8	SL	1.16	0.16	7.19	17	30	4.47
	18		Undisturbed	Meadow (site 2)	435	5.4	0.97	159	7.7	SL	0.82	0.11	9.43	18	30	5.25
	18	Farmland	Tilled	Peanut	435	5.4	0.97	159	7.5	LS	1.03	0.13	7.96	17	30	4.75
	18		Tilled	Mung bean	435	5.4	0.97	159	7.6	SL	1.17	0.15	7.73	17	31	5.75
	18		Tilled	Corn	435	5.4	0.97	159	7.8	SL	1	0.12	8.69	20	32	5.95

Table A1. Continued.

Location	No.	Land use type	Management practices	Vegetation type	MAP	MAT	RDI	ELE	pH	Soil texture	C	N	C : N	SWC	WHC	IN
Yaojingzi	19	Rangeland	Undisturbed	Meadow	434	5.4	0.97	165	8.4	SL	2.21	0.23	9.66	23	34	8.38
Yaojingzi	20	Artificial grassland	Tilled	Meadow (site 1)	433	5.4	0.97	140	8.1	SL	1.85	0.19	9.91	14	33	6.44
	20		Tilled	Meadow (site 2)	433	5.4	0.97	140	8.1	SL	1.9	0.19	9.98	12	33	5.62
	20	Farmland	Tilled	Corn	433	5.4	0.97	140	8.1	SL	0.92	0.1	9.23	18	32	8.23
Wulanaodu	21	Rangeland	Undisturbed	Meadow (site 1)	442	5.3	0.93	152	8.1	SL	1.25	0.16	7.89	22	33	4.23
	21		Undisturbed	Meadow (site 2)	442	5.3	0.93	152	8.1	SL	1.3	0.16	8.03	19	34	4.87
	21	Farmland	Tilled	Corn	442	5.3	0.93	152	8.2	SL	1.74	0.24	7.02	20	32	4.12
	21	Woodland	Undisturbed	Wood and shrub	442	5.3	0.93	152	7.5	SL	1.87	0.23	8.11	20	34	6.55
Chaganhua	22	Rangeland	Undisturbed	Meadow (site 1)	467	5.1	0.93	202	8.5	LS	1.54	0.2	7.67	24	36	4.32
	22		Undisturbed	Meadow (site 2)	467	5.1	0.93	202	8.4	LS	1.42	0.19	7.44	22	36	5.01
Wulantuga	23	Rangeland	Undisturbed	Meadow	472	5.1	0.91	291	8.5	SL	2.16	0.2	10.63	23	34	4.85
	23	Farmland	Tilled	Corn	472	5.1	0.91	291	8.2	SL	1.73	0.24	7.36	22	33	7.75
	23		Tilled	Peanut	472	5.1	0.91	291	7.9	SL	1.72	0.23	7.76	22	32	3.52
	23	Woodland	Undisturbed	Wood and shrub	472	5.1	0.91	291	7.8	SL	1.63	0.19	8.75	18	35	7.39

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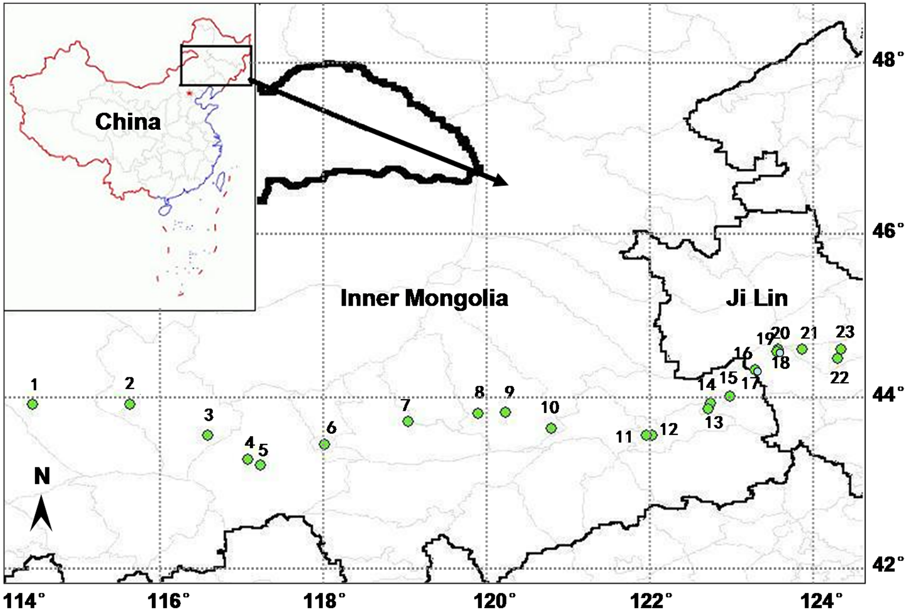

Figure 1. Sample locations (1–23; see Table 1) at a regional scale in northeast China.

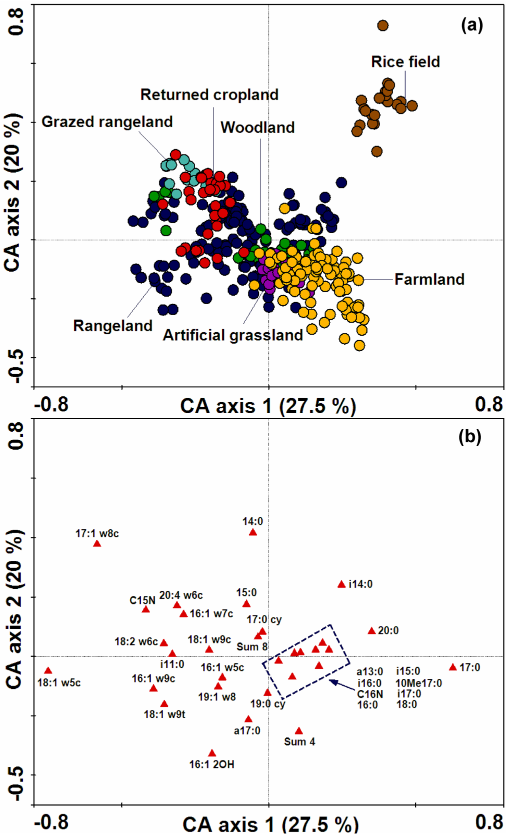

Figure 2. Ordination plots of correspondence analysis (CA) of all samples and fatty acids. **(a)** Ordination plot of 451 samples scores across 7 land use types (rangeland, artificial grassland, grazed rangeland, farmland, returned cropland, woodland, rice field); **(b)** ordination plot of 31 fatty acids scores. The fatty acids scores are near the points for samples in which they occur with the highest relative contributions.

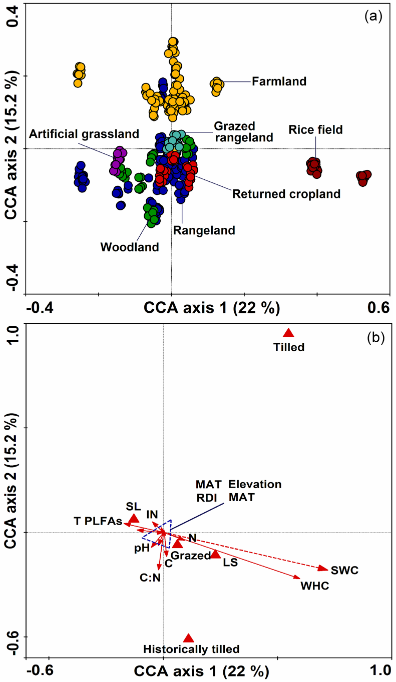

Figure 3. Ordination plots of canonical correspondence analysis (CCA) of all samples and environmental factors. **(a)** Ordination plot of 451 samples scores across 7 land use types; **(b)** Ordination plot of habitat and management factors scores, in which spatial structure were run as covariates. Mean annual temperature (MAT), mean annual precipitation (MAP), radiative dry index (RDI), elevation, soil water content (SWC, including natural precipitation and managed inputs), soil inorganic N (IN), soil total C and N (C, N), soil C : N, total (T) PLFAs, water holding capacity (WHC) and soil pH were quantitative environmental factors, and soil texture (loamy sand, LS; sandy loam, SL), land management practices (tilled, historically tilled, grazed) were qualitative (nominal) environmental factors. Quantitative factors were plotted as vectors, and qualitative factors were plotted as centroids.

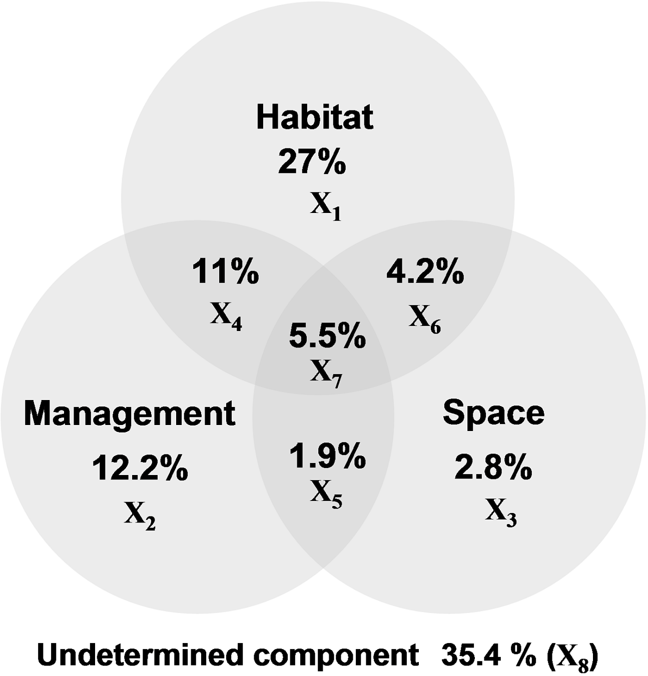

Figure 4. Variation partitioning procedure of microbial community composition, explained by habitat (mean annual temperature and precipitation, radiative dry index, elevation, soil texture, pH, soil C and N content, soil C : N, inorganic N, total PLFAs, water holding capacity), land management (tilled, historically tilled, grazed practices) and spatial structure (x, y, xy, x^2, y^2, x^2y, xy^2, x^3, y^3; the nine terms which latitudinal (x) and longitudinal (y) coordinate were used to calculate a cubic trend surface) factors.

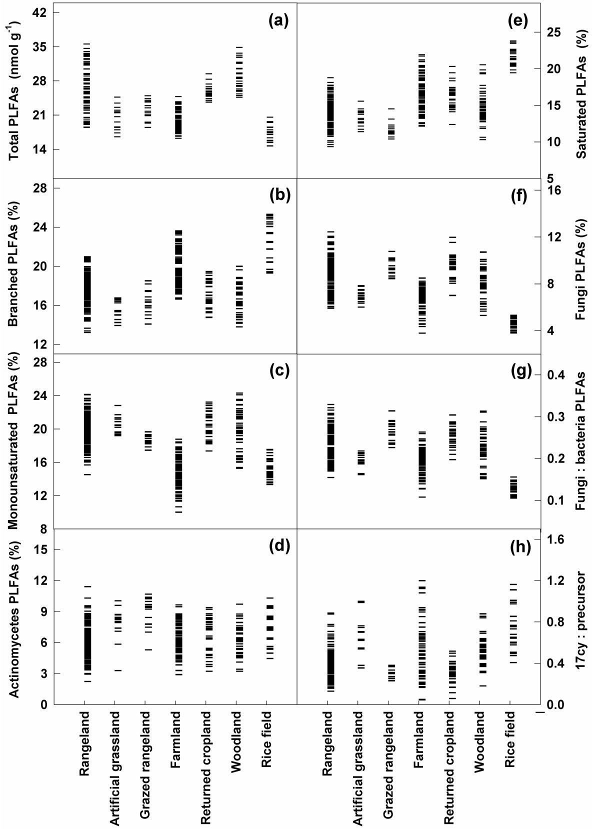

Figure 5. Soil microbial biomass (i.e. total PLFAs), percentages of branched PLFAs (gram-positive bacteria), monounsaturated PLFAs (gram-negative bacteria), actinomycetes (10Me), saturated PLFAs (i.e. common in microorganism), fungi (F), fungal : bacterial PLFAs (F : B) and 17cy:precursor across 7 land use types at a regional scale of northeastern China.