# Soil moisture and land use are major determinants of soil microbial community composition and biomass at a regional scale in northeastern China

**Linna Ma[1], Chengyuan Guo [1], Xiaotao Lü[3], Shan Yuan[1, 2], Renzhong Wang [1,*]**

[1] State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, 100093, China
[2] University of Chinese Academy of Sciences, Beijing, 100049, China
[3] State Key Laboratory of Forest and Soil Ecology, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, 110164, China

*Corresponding author

Email: wangrz@ibcas.ac.cn Tel: +86-10-62836550 Fax: +86-10-82595962

Manuscript type: Research article

Short running title: Regional patterns of soil microbial community composition

Number of tables: 2 Number of figures: 5

Supporting information: 1

## Abstract

Global environmental factors impact soil microbial communities, and further affect organic matter decomposition, nutrient cycling and vegetation dynamic. However, little is known about the relative contributions of climate factors, soil properties, vegetation types, land management practices and spatial structure (serve as a proxy for underlying effects of temperature and precipitation for spatial variation) on soil microbial community composition and biomass at large spatial extents. Here, we compared soil microbial communities using phospholipid fatty acid method across 7 land use types from 23 locations at a regional scale in northeastern China (850 × 50 km). The results showed that soil moisture and land use changes were most closely related to microbial community composition and biomass at the regional scale, while soil total C content and climate effects were weaker but still significant. Factors such as spatial structure, soil texture, nutrient availability and vegetation types were not important. Higher contributions of gram-positive bacteria were found in wetter soils, whereas higher contributions of gram-negative bacteria and fungi were observed in drier soils. The contributions of gram-negative bacteria and fungi were lower in heavily disturbed soils than historically disturbed and undisturbed soils. The lowest microbial biomass appeared in the wettest and driest soils. In conclusion, dominant climate and soil properties were not the most important drivers governing microbial community composition and biomass because of inclusion of irrigated and managed practices, and thus soil moisture and land use appear to be primary determinants of microbial community composition and biomass at the regional scale in northeastern China.

# 1 Introduction

Soil microbial community plays important roles in regulating organic matter decomposition, nutrient cycling, soil structural formation, and even plant interactions (Wardle et al., 2004; Harris et al., 2009). Meanwhile, it is subjected to the influences of environmental conditions, land use and spatial structure (Yang et al., 2013). Although there is a growing body of evidence indicates that climate, soil property, vegetation, spatial structure and land use as the most important determinants of the global and regional patterns in soil microbial communities (Kreft and Jetz, 2007; Nielsen et al., 2010; Zinger et al., 2011; Pasternak et al., 2013; Tsiknia et al., 2014), teasing apart the contributions of multiple drivers on microbial community composition and biomass remains unclear.

Regional climate factors exert major influences on distributions of microbial communities by determining temperature and soil water availability along topographic gradients (Hackl et al., 2005; Carletti et al., 2009; Brockett et al., 2012). Drenovsky et al. (2010) and Brockett et al. (2012) found that soil water availability was an important determinant of microbial community composition, and fungal: bacterial biomass ratios decreased with increased soil water saturation at regional scales. In different types of natural Austrian forests, Hackl et al. (2005) showed that mean annual temperature was the major factor influencing microbial community composition in zonal forest, but soil water availability was most closely correlated with microbial community in azonal forests.

Soil property has been found strongly correlate with soil microbial community structure and abundance at the regional extents. Previous studies have reported that soil texture, organic matter

content, N availability and pH exhibited the dominant effects on soil microbial community composition, while climatic effects were weaker but still significant at regional scales (Šantrucková et al., 2003; Brockett et al. 2012; Yang et al. 2013; Tsiknia et al. 2014). For example, Tsiknia et al. (2014) reported that soil total organic C, pH and geographic distance being identified as the most important determinants of microbial community abundance at the watershed scale in Greece. Moreover, 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).

Spatial structure (serve as a proxy for underlying effects of temperature and precipitation for spatial variation) influences the organization of community as a functional variable, other than the background in which biological and environmental factors act on community and ecosystem (Borcard et al., 1992). Recent researches have showed that strong autocorrelations were set between microbial groups, and geographic distance could explain a high proportion of microbial community variation (Tsiknia et al., 2014). However, Fierer and Jackson (2006) claimed that soils with similar environmental characteristics have similar bacterial communities regardless of geographic distance at continental scales. Using spatial trend surface analysis, Drenovsky et al. (2010) also found that spatial structure did not influence microbial community composition across three biogeographical provinces in Califorina.

At regional scales, land use change is the major reason for spatial heterogeneity. It has been

89 shown that land use changes would lead to great variation in soil microbial community
90 composition in diverse ecosystems (Drenovsky et al., 2010), though their impacts depend on
91 many factors, including the original vegetation that is being replaced, and associated land
92 management practices such as tillage, fallow periods, and related water and nutrient applications,
93 such as irrigation and fertilization (Scanlon et al., 2007; Ma et al., 2013; Yang et al., 2013; Chen
94 et al., 2014). In one study, Drenovsky et al. (2010) reported that distinct microbial communities
95 were associated with land use types and disturbance at the regional scale in California. Tillage
96 influences multiple soil physical and chemical properties, disrupts soil fungal hyphae (Evans and
97 Miller, 1990), and alters microbial community composition (Ingram et al., 2008; Drenovsky et
98 al., 2010). Recently, changes in land use have occurred in temperate area of northeast China as a
99 result of expansion of farmlands and grazed rangelands at the expense of natural habitats,
100 however, little is known about soil microbial community composition to land use changes at
101 regional extents.
102 In this study we compare microbial community composition and biomass from 23 locations
103 across 7 land use types (i.e. rangeland, artificial grassland, grazed rangeland, farmland, returned
104 cropland, woodland, rice field) at a regional scale in Northeast China Transect (NECT). The
105 NECT is identified as a mid-latitude semiarid terrestrial transect and is sensitive to climate
106 change and disturbance, thus provides an ideal setting to investigate distribution patterns of soil
107 microbial community. Our work specially aimed at teasing apart the contributions of climate,
108 soil properties, vegetation types, spatial structure and land use on microbial community
109 composition and biomass at the regional scale. We hypothesize that climate and soil properties

110 are the primary drivers to affect soil microbial community composition and biomass because
111 climatic gradient, especially precipitation, is one of the most notable features at this region
112 (Wang et al., 2003).
113
114 # 2 Materials and Methods
115 ## 2.1 Study locations
116 The field study was conducted on a regional scale (43°12′ – 44°36′ N; 114°34′ – 124°18′ E)
117 across Jilin province and Inner Mongolia (about 850 km from east to west, and 50 km from north
118 to south) with 23 locations in North-east China Transect (NECT) (Table 1, Fig. 1). The NECT
119 was identified as a core project of International Geosphere-Biosphere Programme (IGBP) which
120 represents an array of regional-scale gradients on all continents that vary in major environmental
121 variables (Koch et al., 1995). This area has a continental monsoon climate, with large seasonal
122 temperature and precipitation gradients. Long-term (1950 – 2000) mean annual temperature,
123 precipitation and radiative dry index at this spatial scale range from approximately 1.3 – 6.8 °C,
124 237 – 472 mm and 0.91 – 1.44, respectively. The elevation gradients range from 140 m to 1309
125 m (http: //www. worldclim. com; Zhang et al., 1997; Appendix S1). Mean soil total C, N and C:
126 N varied 3.3-fold, 2.4-fold and 2.7-fold across the region. Overall, there were 7.4-fold and
127 2.8-fold differences in soil water content and water holding capacity, whereas soil origin and pH
128 differed slightly (Appendix S1).
129 Spatial climatic variability, especially precipitation, is one of the most notable features of the
130 transect. Due to the large 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; Appendix S1). 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 Table 1, Appendix S1, 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 × 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.

152 **2.3 Soil microbial community analysis**

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

165 Thirty-one fatty acids were included in the analyses. (1) branched fatty acids indicative of
166 gram-positive bacteria: a13: 0, i14: 0, i15: 0, i16: 0, i17: 0 and a17: 0; (2) monounsaturated fatty
167 acids indicative of gram-negative bacteria: 16: 1ω7c, 17: 1ω8c, 18: 1ω5c, 18: 1ω9t, 17: 0cy and
168 19: 0cy (Frostegård et al., 1993, 1996); (3) saturated fatty acid (common in soil microorganism):
169 14: 0, 15: 0, 16: 0, 17: 0, 18: 0 and 20: 0; (4) two fatty acids (18: 2ω6c, 18: 1ω9c) were chosen to
170 represent the fungi (Frostegård et al., 2011); (5) actinomycetes was represented by 10Me 17: 0
171 fatty acid. The fatty acids 14: 2ω6c and 14: 1ω8c were unique in three samples which were
172 excluded in the data set. The ratio of 17: 0cy (17cy) to 16: 1ω7c (precursor) was used to as an

173 indicator of physiological stress (Knivett and Cullen, 1965). The viable microbial biomass was
174 calculated by summing concentration of all fatty acids detected in each soil samples (White et al.,
175 1979). Total percentages of fatty acid identified for each microbial group was calculated to
176 represent their relative contributions to the total microbial biomass. The fungal: bacterial fatty
177 acid (gram-positive + gram-negative bacteria) was also included in the data analysis (Frostegård
178 et al., 1996).
179
180 **2.4 Soil property analyses**
181 Soil inorganic N ($NH_4^+$-N + $NO_3^-$-N) was extracted with 2M KCl solution, and the extractant
182 was determined using a flow injection autoanalyzer (FIAstar 5000, Denmark). Soil pH was
183 measured at a soil: water ratio of 1: 2.5 with a pH electrode (PHS 29, China). Soil total C and N
184 content were measured by elemental analyzer (Elemetaranalysator vario Max CN, Germany).
185 Soil texture was determined by the optical size analyzer (Mastersizer 2000, England).
186 Gravimetric soil water content was measured by oven-drying samples at 105 °C for 24 h. Soil
187 water holding capacity was measured by Wilcox method (Wilcox, 1962).
188
189 **2.5 Statistical analyses**
190 Unconstrained ordination−correspondence analysis (CA) was used to compare soil microbial
191 communities among samples ($n$ = 451) using the Canoco for Windows 4.5 package (Ithaca, NY,
192 USA). CA is an indirect gradient analysis method which can provide the basic overview of soil
193 samples, and maximize the correlation between fatty acids and samples (Lepš and Smilauer,

194 2003). Constrained ordination−canonical correspondence analysis (CCA) was used to represent
195 the relationships among environmental factors (habitat, land management, spatial structure),
196 sample patterns, and fatty acids distributions (Lepš and Smilauer, 2003). Qualitative factors were
197 coded for the program using a set of 'dummy factors'. That is, if a sample has a particular value
198 of the factor, then the corresponding dummy factor has the value 1.0, and the other dummy
199 factors have a value of 0.0 for the same sample.
200 In order to separate the effects of environmental factors on microbial communities, the
201 variation partitioning procedure with CCA were used in the analysis (Borcard et al., 1992). The
202 environmental factors were divided into three groups: (1) habitat (mean annual temperature,
203 mean annual precipitation, radiative dry index, elevation, soil texture, pH class, soil N
204 availability, soil C and N content, soil C: N, water holding capacity); (2) land management
205 (tillage, grazing, historically tillage, flooding); (3) spatial structure (x, y, xy, $x^2$, $y^2$, $x^2y$, $xy^2$, $x^3$,
206 $y^3$). The third group consisted of nine terms, in which latitudinal (x) and longitudinal (y)
207 coordinate were used to calculate a cubic trend surface. Spatial trend surface analysis is one of
208 the quantitative ecological methods that study the relation between spatial structure and species
209 abundance distribution in community (Legendre, 1990). The variation partitioning procedure
210 decomposed the total variability into eight parts: individual effect of habitat ($X_1$), land
211 management ($X_2$), spatial structure ($X_3$), combined effects of habitat and land management ($X_4$),
212 combined effects of land management and spatial structure ($X_5$), combined effects of habitat and
213 spatial structure ($X_6$), combined effects of the three groups of environmental factors ($X_7$), and
214 residual variation ($X_8$). A complete explanation of these partitioning analyses can be found in

215 Lepš and Smilauer (2003).

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

221

222 # 3 Results

223 ## 3.1 Variation of soil microbial communities

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

233 The second axis of CA ordination described 20 % of the variation of the composition, mainly
234 associated with management practices and spatial variation. In heavily disturbed habitat, the
235 positions of flood-irrigated rice field and farmland were separated along the second axis (Fig.

236 2a).

237

238 **3.2 Relationship between microbial communities and environmental factors**

239 Soil microbial community composition across 7 land use types at the regional scale was
240 distinguished by environmental factors with the CCA ordination (Fig. 3a, b). The first axis
241 explained 22 % of the variation in microbial community composition, mainly associated with
242 water regime (i.e. soil water availability) and water holding capacity. The second axis described
243 15.2 % of the variation, primarily related to management intensity (tillage > historically tillage
244 or grazing). Climate factors (mean annual precipitation and temperature, radiative dry index,
245 elevation) did not show strong relationships with distribution of microbial communities. Factors
246 such as soil texture (sandy loam), soil inorganic N content and pH plotted near the origin, thus
247 would not be the major drivers of microbial community composition (Fig. 3b).

248

249 **3.3 Variation partitioning**

250 Forward selection of the three groups of environmental factors with CCA suggested that the soil
251 microbial community composition was significantly related to the habitat ($X_1$) (mean annual
252 precipitation and temperature, radiative dry index, elevation, soil texture, pH, soil nutrient
253 content, water holding capacity) and land management ($X_2$) (tillage, grazing, historically tillage,
254 flooding). The variation partitioning procedure showed that total explained variation of microbial
255 community composition was 69.9 % ($X_1$+$X_2$+$X_3$+$X_4$+$X_5$+$X_6$+$X_7$) and undetermined variation of
256 it was 30.1 % ($X_8$) (Fig. 4). The largest unique fraction in the explained variation was the effect

257 of habitat ($X_1$: 27 %), which had a strong overlap with land management ($X_4$: 15 %). In addition,
258 the land management effect was also considerable ($X_2$: 13.4 %), whereas the unique effect of
259 spatial structure ($X_3$: 2.8 %) was very small and statistically not significant.
260
261 **3.4 Soil microbial biomass and contributions of microbial group**
262 Soil microbial biomass (i.e. total PLFAs) varied 2.4-fold across all the land use types at this
263 region ($P < 0.05$, One-way ANOVAs; Fig. 5a). The highest value appeared in one of the
264 rangelands (*c.* 35 nmol $g^{-1}$), and the lowest value appeared in rice field (*c.* 16 nmol $g^{-1}$). Total
265 PLFAs in artificial grassland, grazed rangeland, farmland and returned cropland had
266 intermediate values.
267 Contribution of each microbial group across 7 land use types varied significantly, except that
268 of actinomycetes. Higher contributions of gram-positive bacteria were found in wetter soils,
269 whereas higher contributions of gram-negative bacteria and fungi were observed in drier soils.
270 The contributions of gram-negative bacteria and fungi were lower in heavily disturbed soils than
271 historically disturbed and undisturbed soils ($P < 0.05$, One-way ANOVAs; Fig. 5a-f). Similar to
272 the variation of fungi, the highest fungal: bacterial PLFAs (*c.* 0.35) were appeared in one of the
273 rangelands, and the lowest value occurred in rice field (*c.* 0.15) (Fig. 5g). Surprisingly, 17cy:
274 precursor (used as an indicator of the anaerobic stress) across 7 land use types fluctuated
275 disorderly at this regional scale (Fig. 5h).
276 Stepwise multiple regression analysis demonstrated that 54 % of the variation in microbial
277 community composition could be explained by soil moisture and tillage. Soil moisture, soil total

C content and radiative dry index together accounted for 32 % of the spatial variation in total microbial biomass. Soil moisture alone contributed to 57 % and 57 % of the variation in the contributions of branched and monounsaturated PLFAs, respectively. In this region, radiative dry index, soil moisture and tillage together accounted for 77 % and 65 % of the variation in contribution of fungal PLFAs and fungal: bacterial PLFAs. 38 % of the spatial variability in contribution of bacterial PLFAs could be attributable to the combination of precipitation, soil total C content, water holding capacity and tillage (Table 2).

## 4 Discussion

Exploring the primary drivers regulating distributions of soil microbial communities and teasing apart relative contributions of multiple environmental factors (e.g. climate, soil texture, pH, soil organic matter content, vegetation type), land management practices and spatial structure on microbial community composition and biomass are important challenges in microbial ecology. In this study, soil moisture is a main control on microbial communities across 7 land use types at the regional scale, which explained 31 % of the variation in microbial community composition (Fig. 4; Table 2). Drier soils were more enriched in gram-negative bacteria and fungi, whereas wetter soils were more enriched in gram-positive bacteria (Fig. 5). These findings are in agreement with the previous observations (Rinklebe and Langer, 2006; Entry et al., 2008; Clark et al., 2009; Drenovsky et al., 2010; Ma et al., 2014). The stress of drought likely facilitates fungi to survive better, because soil fungi rely on more aerobic conditions and are more tolerant to drought due to their filamentous nature (Zhang et al., 2005a). The aerobic filamentous fungi

have variable hyphal networks that can relocate water and nutrient resource by cytoplasm translocation (Klein and Paschke, 2004). As soils become water-saturated, reducing soil oxygen levels and creating an environment favorable for facultative and obligate anaerobic bacteria (Drenovsky et al., 2004).

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 because oxygen depletion could trigger conversion of monoenoic fatty acids to cyclopropane fatty acid products (Kieft et al., 1997; Drenovsky et al., 2010). For instance, 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) found that the cyclopropane fatty acids were insensitive to water availability across a large-scale precipitation gradient in California. Similarly, our result also show that the 17cy: precursor responded to high water availability modestly at this region (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 regional scales.

Distinct microbial community composition and biomass are associated with land disturbance levels and management practices at the regional scale in northeast China. 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 (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 (Cookson et al., 2008; Sun et al., 2011). Consistent with other large-scale studies, conventional tillage soils had higher proportions of gram-positive bacteria, and had lower proportions of fungi in this study (Fig. 2b) (Galvez et al., 2001; Zhang et al., 2005a). 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).

Given the strong effects of heavy disturbance on soil microbial communities, 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. These results are supported by observations in other studies (Bardgett and McAlister, 1999; Ingram et al., 2008; Sun et al. 2011). Ingram et al. (2008) reported that long-term light grazing showed no effect on soil organic C content and microbial community composition based on concentrations of PLFA biomarkers in a mixed-grass ecosystem. As the disturbance ceased, 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). However, Buckley and Schmidt (2003) reported that microbial community composition did not differ significantly

between conventionally cultivated fields and fields that had been abandoned from cultivation for nine years. A possible explanation of this result is that long-term sustainable tillage decreases soil C content, thus the recovery of soil organic matter to pre-agricultural levels may require decades or even centuries.

Many previous studies have demonstrated that vegetation types, soil properties and spatial structure can influence soil microbial community function and abundance through providing suitable habitats and food sources (Kourtev et al., 2003; Šantrucková et al., 2003; Han et al., 2007; Chen et al., 2014), whereas our findings of microbial community composition were not related to these factors across this region. In the current study, soils were sampled in different vegetation types and soil nutrient content, but the microbial community composition were very similar at the same geographical location in natural habitats (e.g. meadow versus wood and shrub, data not shown) (Fig. 5). Similar trends were observed in heavily disturbed habitats, the distributions of microbial communities were depended on land disturbance levels and practices rather than agricultural plant species. For example, the farmland soils (e.g. corn, peanut, mung bean, red bean) in the same location clustered together in CCA ordination despite the different plant species that they represented (Fig. 2, 3, 5). These results are consistent with the study of Drenovsky et al. (2010) who reported that microbial community composition was more strongly influenced by disturbance than by agricultural plant species in California.

Habitat factors and land management triggered complex interactive effects on soil microbial community composition at the regional scale in northeastern China, as the value of shared variance fraction was 15 % 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. The significant shared effects in our study could be attributed to the strong effects of land disturbance (e.g. flooding, irrigation, tillage) on soil properties that then affect microbial communities. The findings suggest that land management could partly control soil environmental effects on microbial community composition and biomass at regional scales.

Inconsistent with the hypothesis, soil moisture and land use were the most important factors driving microbial community composition and biomass at the regional scale in northeastern China. In this study, soil moisture 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, pH and vegetation types did not have significant relationships with microbial community composition and biomass. These findings will improve predictions of the ecological processes and consequences of ecosystems under global changes.

**Acknowledgements**

We are grateful for the funding provided by the Natural Science Foundation of China (No. 31170304, 31070228 and 31300440); the four anonymous reviewers for their constructive comments which helped in improving the manuscript.

**References**

Bardgett, R.D., and McAlister, E.: The measurement of soil fungal: bacterial biomass ratios as an

383 indicator of ecosystem self-regulation in temperate meadow grasslands, Biol. Fert. Soils, 29,
384 282 – 290, 1999.
385 Bescansa, P., Imaz, M.J., Virto, I., Enrique, A., and Hoogmoed, W.B.: Soil water retention as
386 affected by tillage and residue management in semiarid Spain, Soil Till. Res., 87, 19 – 27,
387 2006.
388 Borcard, D., Legendre, P., and Drapeau, P.: Partialling out the spatial component of ecological
389 variation, Ecology, 73, 1045 – 1055, 1992.
390 Bossio, D.A., and Scow, K.M.: Impacts of carbon and flooding on soil microbial communities:
391 phospholipid fatty acids profiles and substrate utilization patterns, Microb. Ecol., 35, 265 –
392 278, 1998.
393 Buckley, D.H., and Schmidt, T.M.: Diversity and dynamics of microbial communities in soils
394 from agro-ecosystems, Environ. Microb., 5, 441 – 452, 2003.
395 Carletti, P., Vendramin, E., Pizzeghello, D., Concheri, G., Zanella, A., Nardi, S., and Squartini,
396 A.: Soil humic compounds and microbial communities in six spruce forests as function of
397 parent material, slope aspect and stand age, Plant Soil, 315, 47 – 65, 2009.
398 Chen, D.M., Mi, J., Chu, P.F., Cheng, J.H., Zhang, L.X., Pan, Q.M., Xie, Y.C., and Bai, Y.F.:
399 Patterns and drivers of soil microbial communities along a precipitation gradient on the
400 Mongolian Plateau, Landscape Ecol., doi: 10.1007/s10980-014-9996-z, 2014.
401 Cookson, W.R., Murphy, D.V., and Roper, M.M.: Characterizing the relationships between soil
402 organic matte components and microbial function and composition along a tillage disturbance
403 gradient, Soil Biol. Biochem., 40, 763 – 777, 2008.
404 Drenovsky, R.E., Vo, D., Graham, K.J., and Scow, K.M.: Soil water content and organic carbon
405 availability are major determinants of soil microbial community composition, Microb. Ecol.,
406 48, 424 – 430, 2004.
407 Drenovsky, R.E., Steenwerth, K.L., Jackson, L.E., and Scow, K.M.: Land use and climatic
408 factors structure regional patterns in soil microbial communities, Global Ecol. Biogeogr., 19,
409 27 – 39, 2010.

Eskelinen, A., Stark, S., and Männistö, M.: Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats, Oecologia, 161, 113 – 123, 2009.

Evans, D.G., and Miller, M.H.: The role of the external mycelial network in the effect of soil disturbance upon vesicular–arbuscular mycorrhizal colonization of maize, New Phytol., 114, 65 – 71, 1990.

Entry, J.A., Mills, D., Mathee, K., Jayachandran, K., Sojka, R.E. and Narasimhan G.: Influence of irrigated agriculture on soil microbial diversity, Appl. Soil Ecol., 40, 146 – 154, 2008.

Fierer, N., and Jackson, R.B.: The diversity and biogeography of soil bacterial communities, Pro. Natl. Acad. Sci., 103, 626 – 631, 2006.

Frostegård, A., Bååth, E., and Tunlid, A.: Shifts in the structure of soil microbial communities in limed forests as revealed by phospholipid fatty acid analysis, Soil Biol. Biochem., 25, 723 – 730, 1993.

Frostegård, A., and Bååth, E.: The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil, Biol. Fert. Soils, 22, 59 – 65, 1996.

Frostegård, A., Tunlid, A., and Bååth, E.: Use and misuse of PLFA measurements in soils, Soil Biol. Biochem., 43, 1621 – 1625, 2011.

Galvez, L., Douds, D.D., Drinkwater, L.E., and Wagoner, P.: Effect of tillage and farming system upon VAM fungus populations and mycorrhizas and nutrient uptake of maize, Plant Soil, 228, 299 – 308, 2001.

Han, X.M., Wang, R.Q., Liu, J., Wang, M.C., Zhou, J., and Guo, W.H.: Effects of vegetation type on soil microbial community structure and catabolic diversity assessed by polyphasic methods in North China, J. Environ. Sci., 19, 1228 – 1234, 2007.

Hackl, E., Pfeffer, M., Donat, C., Bachmann, G., and Zechmeister-Boltenstern, S.: Composition of the microbial communities in the mineral soil under different types of natural forest, Soil Biol. Biochem., 37, 661 – 671, 2005.

Harris, J.: Soil microbial communities and restoration ecology: facilitators or followers? Science,

325, 573 – 574, 2009.

Ingram, L.J., Stahl, P.D., Schuman, G.E., Buyer, J.S., Vance, G.F., Ganjegunte, G.K., Welker, J.M., and Derner, J.D.: Grazing impacts on soil carbon and microbial communities in a mixed-grass ecosystem, Soil Sci. Soc. Am. J., 72, 939 – 948, 2008.

Kaiser, C., Fuchslueger, L., Koranda, M., Gorfer, M., Stange, C.F., Kitzler, B., Rasche, F., Strauss, J., Sessitsch, A., Boltenstern, S.Z., and Richter, A.: Plants control the seasonal dynamics of microbial N cycling in a beech forest soil by belowground C allocation, Ecology, 92, 1036 – 1051, 2011.

Kieft, T.L., Wilch, E., O'Connor, K., Ringelberg, D.B., and White, D.C.: Survival and phospholipid fatty acid profiles of surface and subsurface bacteria in natural sediment microcosms, Appl. Environ. Microb., 63, 1531–1542, 1997.

Klein, D.A., and Paschke, M.W.: Filamentous fungi: the indeterminate lifestyle and microbial ecology, Microb. Ecol., 47, 224 – 235, 2004.

Knivett, V.A., and Cullen, J.: Some factors affecting cyclopropane acid formation in *Escherichia coli*., Biochem. J., 96, 771 – 776, 1965.

Koch, G.W., Vitousek, P.M., Steffen, W.L., and Walker, B.H.: Terrestrial transects for global change research, Vegetatio, 121, 53 – 65, 1995.

Kreft, H., and Jetz, W.: Global patterns and determinants of vascular plant diversity, Pro. Natl. Acad. Sci., 104, 5925 – 5930, 2007.

Lepš, J., and Šmilauer, P.: Multivariate analysis of ecological data using canoco, Cambridge University Press, Cambridge, 2003.

Ma, L., Guo, C., Xin, X., Yuan, S., and Wang, R.: Effects of belowground litter addition, increased precipitation and clipping on soil carbon and nitrogen mineralization in a temperate steppe, Biogeosciences, 10, 7361 – 7372, 2013.

Ma, L., Yuan, S., Guo, C., and Wang, R.: Carbon and nitrogen dynamics of native *Leymus chinensis* grasslands along a 1000km longitudinal precipitation gradient in northeastern China, Biogeosciences, 11, 7097 – 7106, 2014.

Ni, J., and Zhang, X.S.: Climate variability, ecological gradient and the northeast China transect (NECT), J. Arid Environ., 46, 313 – 325, 2000.

Nielsen, U.N., Osler, G.H.R., Campbell, C.D., Burslem, D.F.R.P., and van der Wal, R.: The influence of vegetation type, soil properties and precipitation on the composition of soil mite and microbial communities at the landscape scale, J. Biogeogr., 37, 1317 – 1328, 2010.

Pasternak, Z., Al-Ashhab, A., Gatica, J., Gafny, R., Avraham, S., Minz, D., Gillor, O., and Jurkevitch, E.: Spatial and temporal biogeography of soil microbial communities in arid and semiarid regions, PLoS ONE, 8(7), e69705, doi: 10.1371/journal.pone.0069705, 2013.

Rinklebe, J., and Langer, U.: Microbial diversity in three floodplain soils at the Elbe River (Germany), Soil Biol. Biochem., 38, 2144 – 2151, 2006.

Šantrucková, H., Bird, M.I., Kalaschnikov, Y.N., Grund, M., Elhottová, D., and Šimek, M.: Microbial characteristics of soils on a latitudinal transect in Siberia, Global Change Biol., 9, 1106 – 1117, 2003.

Scanlon, B.R., Jolly, I., Sophocleous, M., and Zhang, L.: Global impacts of conversions from natural to agricultural ecosystems on water resources: quantity versus quality, Water Resour. Res., 43, 1 – 18, 2007.

Sun, B., Hallett, P.D., Caul, S., Daniell, T.J., and Hopkins, D.W.: Distribution of soil carbon and microbial biomass in arable soils under different tillage regimes, Plant Soil, 338, 17 – 25, 2011.

Tsiknia, M., Paranychianakis, N.V., Varouchakis, E.A., Moraetis, D., and Nikolaidis, N.P.: Environmental drivers of soil microbial community distribution at the Koiliaris Critical Zone Observatory, Microb. Ecol., 99, 139 – 152, 2014.

Wang, R.Z., and Gao, Q.: Climate-driven changes in shoot density and shoot biomass in *Leymus chinensis* (Poaceae) on the northeast China transect (NECT), Global Ecol. Biogeogr., 12, 249 – 259, 2003.

Wang, R.Z., Huang, W.W., Chen, L., Ma, L.N., Guo, C.Y., and Liu, X.Q.: Anatomical and physiological plasticity in *Leymus chinensis* (Poaceae) along large-scale longitudinal gradient

491 in northeast China, PLoS One, 6(11), e26209, doi:10.1371/journal.pone.0026209, 2011.
492 Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H., and Wall,
493 D.H.: Ecological linkages between aboveground and belowground biota, Science, 304, 1629 –
494 1633, 2004.
495 White, D.C., Davis, W.M., Nickels, J.S., King, J.D., and Bobbie, R.J.: Determination of the
496 sedimentary microbial biomass by extractible lipid phosphate, Oecologia, 40, 51 – 62, 1979.
497 Wilcox, J.C.: Rate of soil drainage following an irrigation: A new concept of the upper limit of
498 available moisture, Can. J. Soil Sci., 42(1), 122 – 128, 1962.
499 Yang, Y.F., Wu, L.W., Liu, Q.Y., Yuan, M.T., Xu, D.P., Yu, H., Hu, Y.G., Duan, J.C., Li, X.Z., He,
500 Z.L., Xue, K., Nostrand, J.V., Wang, S.P., and Zhou, J.Z.: Responses of the functional
501 structure of soil microbial community to livestock grazing in the Tibetan alpine grassland,
502 Global Change Biol., 19, 637 – 486, 2013.
503 Zhang, X.S., Gao, Q., Yang, D.A., Zhou, G.S., Ni, J., and Wang, Q.: A gradient analysis and
504 prediction on the Northeast China Transect (NECT) for global change study, Acta Botanica
505 Sinica, 39, 785 – 799, 1997.
506 Zhang, W., Parker, K.M., Luo, Y., Wan, S., Wallace, L.L., and Hu, S.: Soil microbial responses to
507 experimental warming and clipping in a tallgrass prairie, Global Change Biol., 11, 266 – 277,
508 2005a.
509 Zhang, W.J., Rui, W.Y., Tu, C., Diab, H.G., Louws, F.J., Mueller, J.P., Creamer, N., Bell, M.,
510 Wagger, M.G., and Hu, S.: Responses of soil microbial community structure and diversity to
511 agricultural deintensification, Pedosphere, 15(4), 440 – 447, 2005b.
512 Zhang, N.L., Wan, S.Q., Li, L.H., Bi, J., Zhao, M.M., and Ma, K.P.: Impacts of urea N addition
513 on soil microbial community in a semi-arid temperate steppe in northern China, Plant Soil,
514 311, 19 – 28, 2008.
515 Zinger, L., Lejon, D.P.H., Baptist, F., Bouasria, A., Aubert, S., Geremia, R.A., and Choler, P.:
516 Contrasting diversity patterns of crenarchaeal, bacterial and fungal soil communities in an
517 alpine landscape, PLoS ONE, 6(5), e19950, doi: 10.1371/journal.pone.0019950, 2011.
518

**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 |
| | 22 | | | Meadow (site 2) | 8 |
| Wulantuga | 23 | 44°28′N;124°18′E | Rangeland | Meadow | 8 |
| | 23 | | Farmland | Corn | 6 |
| | 23 | | | Peanut | 6 |
| | 23 | | Woodland | Wood and shrub | 8 |
| | | | | *Total* | **451** |

**Table 2** Results of stepwise multiple regression analyses. Independent variables: soil moisture (%), soil total carbon content (C, %), mean annual precipitation (MAP), radiative dry index (RDI), soil water holding capacity (WHC); Dependent variable: soil microbial community composition (SMCC), 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** |
|---|---|---|---|---|
| **SMCC** | Soil moisture | - | 0.31 | 0.000 |
| | Tillage | - | 0.23 | 0.000 |
| **TPLFAs** | Soil moisture | 6.794 | 0.11 | 0.000 |
| | Soil total C | 0.607 | 0.11 | 0.000 |
| | RDI | -26.893 | 0.10 | 0.000 |
| **BP** | Soil moisture | 0.262 | 0.57 | 0.000 |
| | Tillage | 1.783 | 0.06 | 0.000 |
| **MP** | Soil moisture | -0.105 | 0.57 | 0.000 |
| | Tillage | -3.800 | 0.17 | 0.000 |
| **SP** | Soil moisture | 0.329 | 0.49 | 0.000 |
| | RDI | -3.796 | 0.09 | 0.000 |
| **F** | RDI | 7.074 | 0.57 | 0.000 |
| | Tillage | -1.580 | 0.14 | 0.000 |
| | Soil moisture | -0.042 | 0.06 | 0.000 |
| **B** | MAP | -0.044 | 0.20 | 0.000 |
| | Soil total C | 1.218 | 0.07 | 0.000 |
| | WHC | 0.158 | 0.06 | 0.000 |
| | Tillage | 1.514 | 0.05 | 0.001 |
| **F:B** | RDI | 0.142 | 0.42 | 0.000 |
| | Tillage | -0.033 | 0.12 | 0.000 |
| | Soil moisture | -0.002 | 0.11 | 0.000 |

## Figure legends

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

**Fig. 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.

**Fig. 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.

**Fig. 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, flooded 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.

**Fig. 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 in northeastern China.

**Fig. 1**

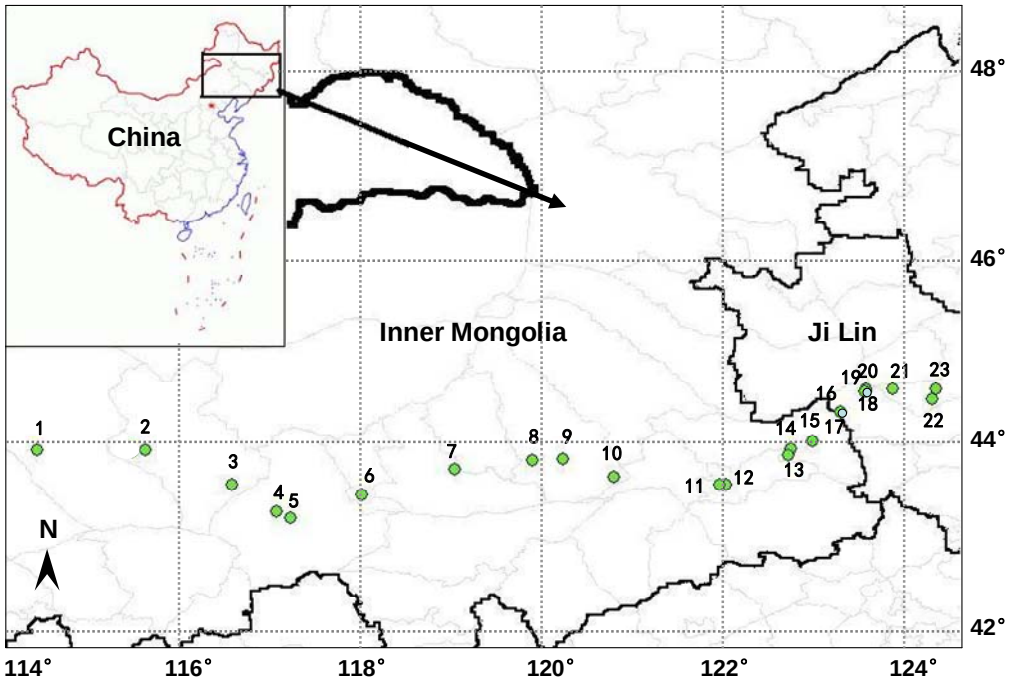

China
Inner Mongolia
Ji Lin
N
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
48°
46°
44°
42°
114°
116°
118°
120°
122°
124°

**Fig. 2**

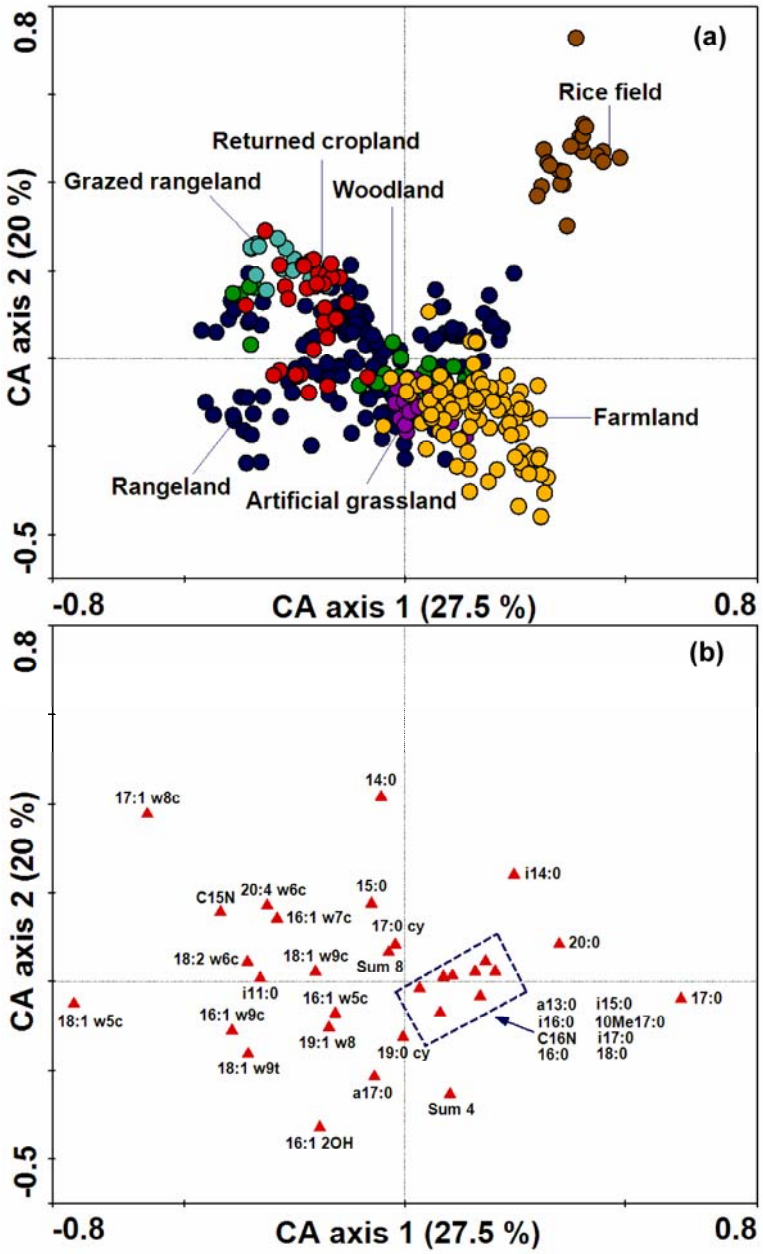

(a)
Rice field
Returned cropland
Grazed rangeland
Woodland
Farmland
Rangeland
Artificial grassland
CA axis 2 (20 %)
CA axis 1 (27.5 %)
0.8
-0.5
-0.8
0.8
(b)
14:0
17:1 w8c
i14:0
C15N
20:4 w6c
15:0
16:1 w7c
17:0 cy
20:0
18:2 w6c
18:1 w9c
Sum 8
i11:0
16:1 w5c
17:0
18:1 w5c
16:1 w9c
a13:0
i16:0
C16N
16:0
i15:0
10Me17:0
i17:0
18:0
19:1 w8
19:0 cy
18:1 w9t
a17:0
Sum 4
16:1 2OH
CA axis 2 (20 %)
CA axis 1 (27.5 %)
0.8
-0.5
-0.8
0.8

**Fig. 3**

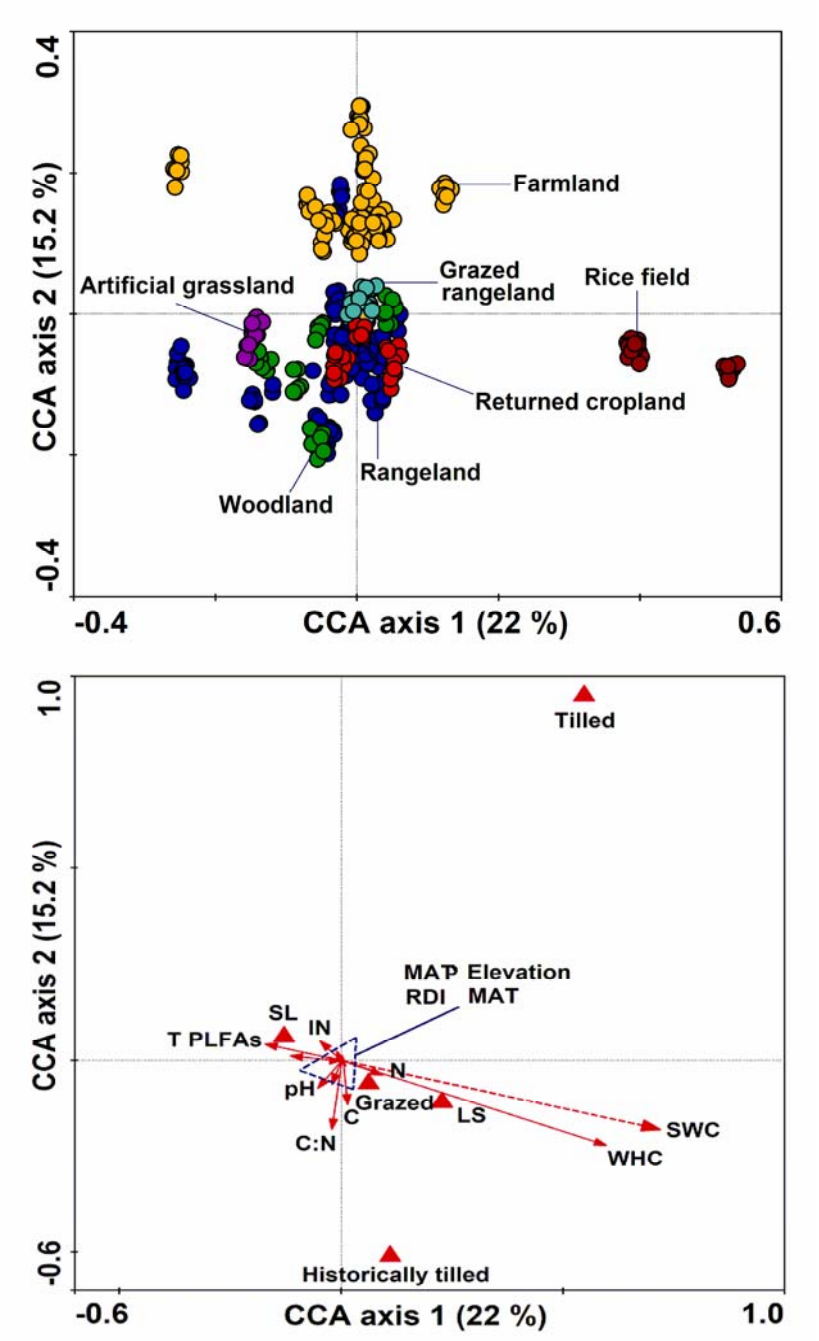

0.4
-0.4
CCA axis 2 (15.2 %)
Farmland
Grazed rangeland
Artificial grassland
Rice field
Returned cropland
Rangeland
Woodland
-0.4
CCA axis 1 (22 %)
0.6
1.0
-0.6
Tilled
MAP
RDI
Elevation
MAT
SL
IN
T PLFAs
N
pH
Grazed
LS
C
SWC
C:N
WHC
Historically tilled
-0.6
CCA axis 1 (22 %)
1.0

**Fig. 4**

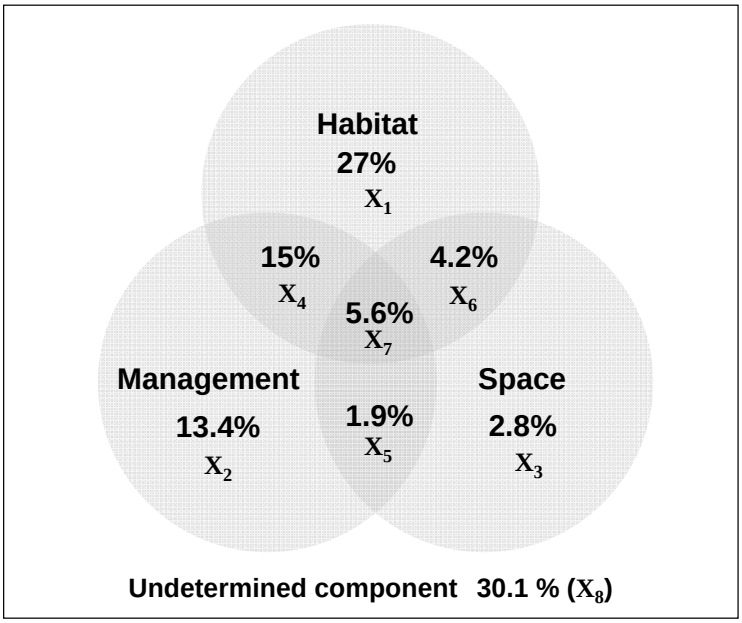
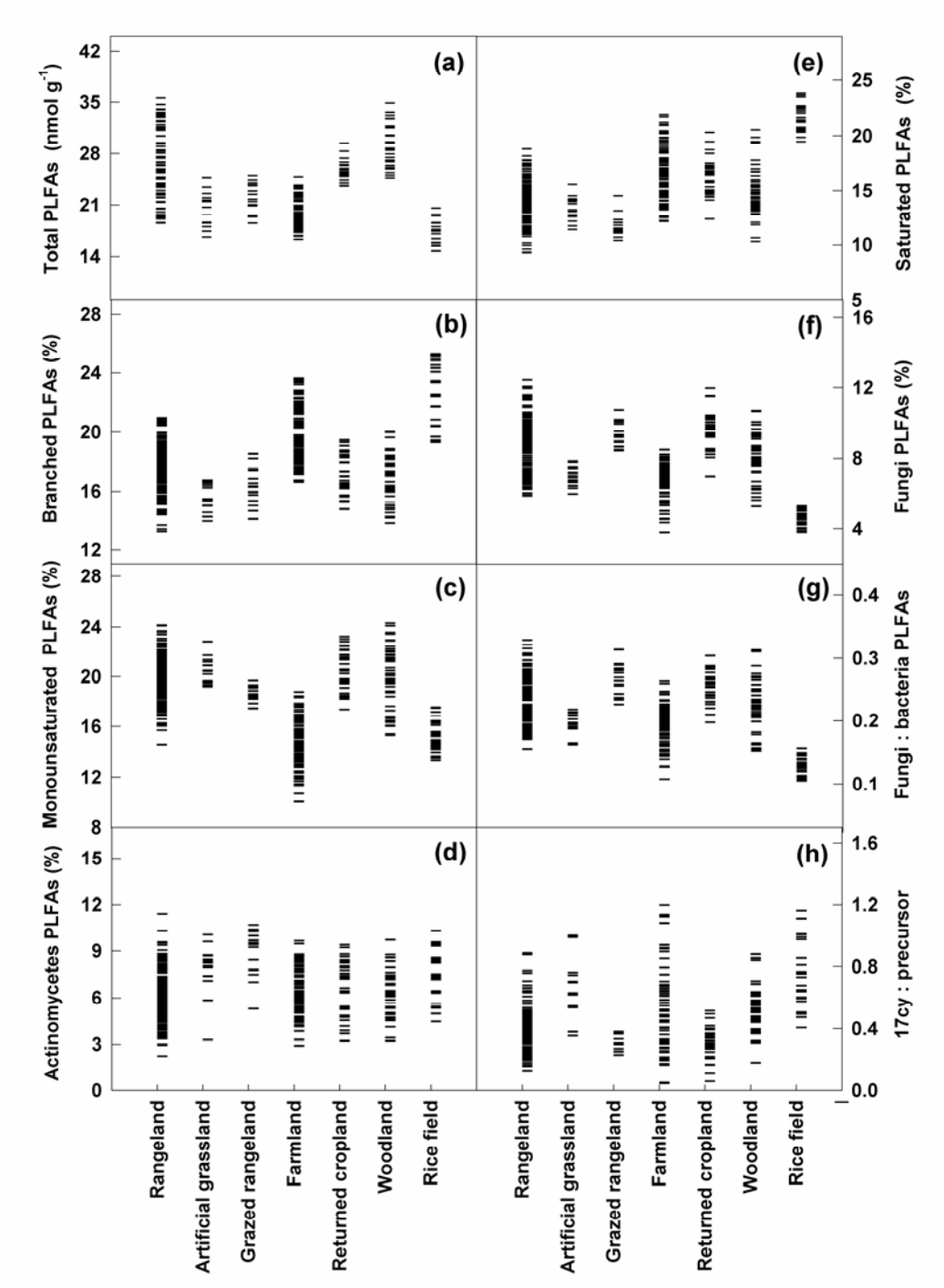

Habitat
27%
X1
15%
X4
4.2%
X6
5.6%
X7
Management
13.4%
X2
1.9%
X5
Space
2.8%
X3
Undetermined component 30.1 % (X8)

**Fig. 5**


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Total PLFAs (nmol g-1)
Branched PLFAs (%)
Monounsaturated PLFAs (%)
Actinomycetes PLFAs (%)
Saturated PLFAs (%)
Fungi PLFAs (%)
Fungi : bacteria PLFAs
17cy : precursor
Rangeland
Artificial grassland
Grazed rangeland
Farmland
Returned cropland
Woodland
Rice field

**Appendix S1** 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 |
| 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 |