

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

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26 **Abstract**

27 Global environmental factors impact soil microbial communities, and further affect organic
28 matter decomposition, nutrient cycling and vegetation dynamic. However, little is known about
29 the relative contributions of climate factors, soil properties, vegetation types, land management
30 practices and spatial structure on soil microbial community composition and biomass at large
31 spatial extents. Here, we compared soil microbial communities using phospholipid fatty acid
32 method across 7 land use types from 23 locations at a regional scale in northeastern China (850 ×
33 50 km). The results showed that soil moisture and land use changes exhibited the dominant
34 effects on microbial community composition and biomass at the regional scale, while soil total C
35 content and climate effects (expressed as a function of large-scale spatial variation) were weaker
36 but still significant. Factors such as spatial structure, soil texture, nutrient availability and
37 vegetation types were not important. Higher contributions of gram-positive bacteria were found
38 in wetter soils, whereas higher contributions of gram-negative bacteria and fungi were observed
39 in drier soils. The contributions of gram-negative bacteria and fungi were lower in heavily
40 disturbed soils than historically disturbed and undisturbed soils. The lowest microbial biomass
41 appeared in the wettest and driest soils. In conclusion, dominant climate and soil properties,
42 commonly known to structure regional distributions of microbial communities, were not the
43 most important drivers governing microbial community composition and biomass because of
44 inclusion of irrigated and managed practices. In comparison, soil moisture and land use appear to
45 be primary determinants of microbial community composition and biomass at the regional scale.

46

47 **1 Introduction**

48 Soil microbial community plays important roles in [regulating](#) organic matter decomposition,
49 nutrient cycling, soil structural formation, and even plant interactions (Wardle et al., [2004](#);
50 Harris et al., 2009). [Meanwhile](#), it is subjected to the influences of environmental conditions,
51 land use and spatial structure (Yang et al., 2013). Although there is a growing body of evidence
52 indicates that climate, soil property, vegetation, spatial structure and land use as the most
53 important determinants of the global and regional patterns in soil microbial communities (Kreft
54 and Jetz, 2007; Nielsen et al., 2010; Zinger et al., 2011; Pasternak et al., 2013; Tsiknia et al.,
55 2014), teasing apart the contributions of multiple drivers on microbial community composition
56 and biomass remains unclear.

57 Regional climate factors exert major influences on distributions of microbial communities by
58 determining temperature and soil water availability along topographic gradients (Hackl et al.,
59 2005; Carletti et al., 2009; Brockett et al., 2012). Drenovsky et al. (2010) and Brockett et al.
60 (2012) found that soil water availability was an important determinant of microbial community
61 composition, and fungal: bacterial biomass ratios decreased with increased soil water saturation
62 at regional scales. In contrast, Hackl et al. (2005) showed that mean annual temperature was the
63 major factor influencing microbial community composition in zonal forest, but soil water
64 availability was most closely correlated with microbial community in azonal Austrian forests.

65 Soil property has been found strongly correlate with soil microbial community structure and
66 abundance at large spatial extents. Previous studies have reported that soil texture, organic
67 matter content, N availability and pH exhibited the dominant effects on soil microbial

68 community composition, while climatic effects were weaker but still significant at regional
69 scales (Šantrůcková et al., 2003; Brockett et al. 2012; Yang et al. 2013; Tsiknia et al. 2014). For
70 example, Tsiknia et al. (2014) reported that soil total organic C, pH and geographic distance
71 being identified as the most important determinants of microbial community abundance at the
72 watershed scale in Greece. Moreover, plant communities differing in species composition are
73 likely to produce litter and that differ in their chemical composition, which may subsequently
74 influence soil microbial community composition (Zhang et al., 2005a; Eskelinen et al., 2009). As
75 a biotic driver, plants may also exert great effects on soil microbial communities by controlling
76 allocation of belowground photosynthates (Kaiser et al., 2011).

77 Spatial structure influences the organization of community as a functional variable, other than
78 the background in which biological and environmental factors act on community and ecosystem
79 (Borcard et al., 1992). Recent researches have showed that strong autocorrelations were set
80 between microbial groups, and geographic distance could explain a high proportion of microbial
81 community variation (Tsiknia et al., 2014). However, Fierer and Jackson (2006) claimed that
82 soils with similar environmental characteristics have similar bacterial communities regardless of
83 geographic distance at continental scales. Using spatial trend surface analysis, Drenovsky et al.
84 (2010) also found that spatial structure did not influence microbial community composition
85 across three biogeographical provinces in California.

86 At regional scales, land use change is the major reason for spatial heterogeneity. It has been
87 shown that land use changes would lead to great variation in soil microbial community
88 composition in diverse ecosystems (Drenovsky et al., 2010), though their impacts depend on

89 many factors, including the original vegetation that is being replaced, and associated land
90 management practices such as tillage, fallow periods, and related water and nutrient applications,
91 such as irrigation and fertilization (Scanlon et al., 2007; Ma et al., 2013; Yang et al., 2013; Chen
92 et al., 2014). In one study, Drenovsky et al. (2010) reported that distinct microbial communities
93 were associated with land use types and disturbance at the regional scale in California. Tillage
94 influences multiple soil physical and chemical properties, disrupts soil fungal hyphae (Evans and
95 Miller, 1990), and alters microbial community composition (Ingram et al., 2008; Drenovsky et
96 al., 2010). Recently, changes in land use have occurred in temperate area of northeast China as a
97 result of expansion of farmlands and grazed rangelands at the expense of natural habitats,
98 however, little is known about soil microbial community composition to land use changes at
99 large spatial scales.

100 In this study we compare microbial community composition and biomass from 23 locations
101 across 7 land use types (i.e. rangeland, artificial grassland, grazed rangeland, farmland, returned
102 cropland, woodland, rice field) at a regional scale in Northeast China Transect (NECT). The
103 NECT is identified as a mid-latitude semiarid terrestrial transect and is sensitive to climate
104 change and disturbance, thus provides an ideal setting to investigate distribution patterns of soil
105 microbial community. Our work specially aimed at teasing apart the contributions of climate,
106 soil property, vegetation, spatial structure and land use on microbial community composition and
107 biomass at the regional scale. We hypothesize that climate and soil properties are the primary
108 drivers to affect soil microbial community composition and biomass because climatic gradient,
109 especially precipitation, is one of the most notable features at this region (Wang et al., 2003).

110 **2 Materials and Methods**

111 **2.1 Study locations**

112 The field study was conducted on a large spatial scale ($43^{\circ}12' - 44^{\circ}36' \text{ N}$; $114^{\circ}34' - 124^{\circ}18' \text{ E}$)
113 across Jilin province and Inner Mongolia (about 850 km from east to west, and 50 km from north
114 to south) with 23 locations in North-east China Transect (NECT) (Table 1, Fig. 1). The NECT
115 was identified as a core project of International Geosphere-Biosphere Programme (IGBP) which
116 represents an array of regional-scale gradients on all continents that vary in major environmental
117 variables (Koch et al., 1995). This area has a continental monsoon climate, with large seasonal
118 temperature and precipitation gradients. Long-term (1950 – 2000) mean annual temperature,
119 precipitation and radiative dry index at this large spatial scale range from approximately 1.3 –
120 6.8°C , 237 – 472 mm and 0.91 – 1.44, respectively. The elevation gradients range from 140 m
121 to 1309 m (<http://www.worldclim.com>; Zhang et al., 1997; Appendix S1). Mean soil total C, N
122 and C: N varied 3.3-fold, 2.4-fold and 2.7-fold across the region. Overall, there were 7.4-fold
123 and 2.8-fold differences in soil water content and water holding capacity, whereas soil origin and
124 pH differed slightly (Appendix S1).

125 Spatial climatic variability, especially precipitation, is one of the most notable features of the
126 transect. Due to the large decrease in precipitation from the east (Jilin province) to the west
127 (Inner Mongolia), vegetation vary gradually from moist meadows in the east to typical steppes
128 and desert steppes in the west with farmlands, returned croplands and woodlands spread evenly
129 across the gradient (Wang et al., 2003, 2011; Appendix S1). All farmlands were irrigated only
130 several times (2 – 3 times) during the growing season, and rice field was flood-irrigated. The

131 large spatial region have remarkable variations in climate, land use types and vegetation types,
132 which make it an ideal region for studying the primary factor that driving soil microbial
133 community composition and biomass. A detailed description of land use types, vegetation types,
134 soil properties can be found in Table 1, Appendix S1, Zhang et al. (1997) and Ni and Zhang
135 (2000).

136

137 **2.2 Soil samplings**

138 451 soil samples from 23 locations including 7 land use types were collected along the NECT in
139 12 – 18 July, 2012. 6 – 16 soil core samples were collected randomly per site (100 × 100 m) for
140 determination of soil microbial communities (Table 1).

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

147

148 **2.3 Soil microbial community analysis**

149 Phospholipid fatty acids (PLFAs) were extracted and quantified from 8.0 g (dry weight
150 equivalent) soils using a procedure described by Bossio and Scow (1998). The separation and
151 identification of extracted PLFAs were carried out according to the standard protocol of the

152 Sherlock Microbial Identification System V_{4.5} (MIDI) and a Gas Chromatograph (Agilent 6850,
153 USA). “A: B ω C” represents the number of carbons in the compound: the number of double
154 bonds in the carbon chain, followed by double bond location from the methyl (ω) end of the
155 molecule (Bossio and Scow, 1998). Cis and trans conformations are indicated by the suffixes c
156 and t. The prefixes a and i indicate anteiso and iso branching; 10Me specifies a methyl group on
157 the 10th carbon from the carboxyl end of the molecule; OH indicates a hydroxyl group; and cy
158 indicates cyclopropane fatty acids. In addition, the fatty acids “sum” indicates imperfect peak
159 separation occurs, and refers two or more fatty acids having the same retention time (Drenovsky
160 et al., 2004).

161 Thirty-one fatty acids were included in the analyses. (1) branched fatty acids indicative of
162 gram-positive bacteria: a13: 0, i14: 0, i15: 0, i16: 0, i17: 0 and a17: 0; (2) monounsaturated fatty
163 acids indicative of gram-negative bacteria: 16: 1 ω 7c, 17: 1 ω 8c, 18: 1 ω 5c, 18: 1 ω 9t, 17: 0cy and
164 19: 0cy (Frostegård et al., 1993, 1996); (3) saturated fatty acid (common in soil microorganism):
165 14: 0, 15: 0, 16: 0, 17: 0, 18: 0 and 20: 0; (4) two fatty acids (18: 2 ω 6c, 18: 1 ω 9c) were chosen to
166 represent the fungi (Frostegård et al., 2011); (5) actinomycetes was represented by 10Me 17: 0
167 fatty acid. The fatty acids 14: 2 ω 6c and 14: 1 ω 8c were unique in three samples which were
168 excluded in the data set. The ratio of 17: 0cy (17cy) to 16: 1 ω 7c (precursor) was used to as an
169 indicator of physiological stress (Knivett and Cullen, 1965). The viable microbial biomass was
170 calculated by summing concentration of all fatty acids detected in each soil samples (White et al.,
171 1979). Total percentages of fatty acid identified for each microbial group was calculated to
172 represent their relative contributions to the total microbial biomass. The fungal: bacterial fatty

173 acid (gram-positive + gram-negative bacteria) was also included in the data analysis (Frostegård
174 et al., 1996).

175

176 **2.4 Soil property analyses**

177 Soil inorganic N ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$) was extracted with 2M KCl solution, and the extractant
178 was determined using a flow injection autoanalyzer (FIAstar 5000, Denmark). Soil pH was
179 measured at a soil: water ratio of 1: 2.5 with a pH electrode (PHS 29, China). Soil total C and N
180 content were measured by elemental analyzer (Elementaranalytator vario Max CN, Germany).
181 Soil texture was determined by the optical size analyzer (Mastersizer 2000, England).
182 Gravimetric soil water content was measured by oven-drying samples at 105 °C for 24 h. Soil
183 water holding capacity was measured by Wilcox method (Wilcox, 1962).

184

185 **2.5 Statistical analyses**

186 Unconstrained ordination—correspondence analysis (CA) was used to compare soil microbial
187 communities among samples ($n = 451$) using the Canoco for Windows 4.5 package (Ithaca, NY,
188 USA). CA is an indirect gradient analysis method which can provide the basic overview of soil
189 samples, and maximize the correlation between fatty acids and samples (Lepš and Smilauer,
190 2003). Constrained ordination—canonical correspondence analysis (CCA) was used to represent
191 the relationships among environmental factors (habitat, land management, spatial structure),
192 sample patterns, and fatty acids distributions (Lepš and Smilauer, 2003). Qualitative factors were
193 coded for the program using a set of ‘dummy factors’. That is, if a sample has a particular value

194 of the factor, then the corresponding dummy factor has the value 1.0, and the other dummy
195 factors have a value of 0.0 for the same sample.

196 In order to separate the effects of environmental factors on microbial communities, the
197 variation partitioning procedure with CCA were used in the analysis (Borcard et al., 1992). The
198 environmental factors were divided into three groups: (1) habitat (mean annual temperature,
199 mean annual precipitation, radiative dry index, elevation, soil texture, pH class, soil N
200 availability, soil C and N content, soil C: N, water holding capacity); (2) land management
201 (tillage, grazing, historically tillage, [flooding](#)); (3) spatial structure (x , y , xy , x^2 , y^2 , x^2y , xy^2 , x^3 ,
202 y^3). The third group consisted of nine terms, in which latitudinal (x) and longitudinal (y)
203 coordinate were used to calculate a cubic trend surface. [Spatial trend surface analysis is one of](#)
204 [the quantitative ecological methods that study the relation between spatial structure and species](#)
205 [abundance distribution in community](#) (Legendre, 1990). The variation partitioning procedure
206 decomposed the total variability into eight parts: individual effect of habitat (X_1), land
207 management (X_2), spatial structure (X_3), combined effects of habitat and land management (X_4),
208 combined effects of land management and spatial structure (X_5), combined effects of habitat and
209 spatial structure (X_6), combined effects of the three groups of environmental factors (X_7), and
210 residual variation (X_8). A complete explanation of these partitioning analyses can be found in
211 Lepš and Smilauer (2003).

212 Stepwise multiple linear analyses were used to determine the relationships of soil microbial
213 [community composition](#), biomass or contribution of each microbial group with environmental
214 factors. Differences among the sites in soil microbial biomass and contribution of each microbial

215 group were tested using One-way ANOVAs. Data management and statistical analyses were
216 performed using SPSS 17.0 software (SPSS, Chicago, IL, USA).

217

218 **3 Results**

219 **3.1 Variation of soil microbial communities**

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

229 The second axis of CA ordination described 20 % of the variation of the composition, mainly
230 **associated with** management practices and spatial variation (expressed as underlying effects of
231 soil properties). In heavily disturbed habitat, **the positions of** flood-irrigated rice field **and**
232 farmland were separated along the second axis (Fig. 2a).

233

234 **3.2 Relationship between microbial communities and environmental factors**

235 Soil microbial community composition across 7 land use types at the regional scale was

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

244

245 **3.3 Variation partitioning**

246 Forward selection of the three groups of environmental factors with CCA suggested that the soil
247 microbial community composition was significantly related to the habitat (X_1) (mean annual
248 precipitation and temperature, radiative dry index, elevation, soil texture, pH, soil nutrient
249 content, water holding capacity) and land management (X_2) (tillage, grazing, historically tillage,
250 flooding). The variation partitioning procedure showed that total explained variation of microbial
251 community composition was 69.9 % ($X_1+X_2+X_3+X_4+X_5+X_6+X_7$) and undetermined variation of
252 it was 30.1 % (X_8) (Fig. 4). The largest unique fraction in the explained variation was the effect
253 of habitat (X_1 : 27 %), which had a strong overlap with land management (X_4 : 15 %). In addition,
254 the land management effect was also considerable (X_2 : 13.4 %), whereas the unique effect of
255 spatial structure (X_3 : 2.8 %) was very small and statistically not significant.

256

257 **3.4 Soil microbial biomass and contributions of microbial group**

258 **Soil microbial biomass (i.e. total PLFAs)** varied 2.4-fold across all the land use types at this
259 region ($P < 0.05$, One-way ANOVAs; Fig. 5a). The highest value appeared in one of the
260 rangelands (*c.* 35 nmol g⁻¹), and the lowest value appeared in rice field (*c.* 16 nmol g⁻¹). Total
261 PLFAs in artificial grassland, grazed rangeland, farmland and returned cropland had
262 intermediate values.

263 Contribution of each microbial group across 7 land use types varied significantly, except that
264 of actinomycetes. **Higher contributions of gram-positive bacteria were found in wetter soils,**
265 **whereas higher contributions of gram-negative bacteria and fungi were observed in drier soils.**
266 **The contributions of gram-negative bacteria and fungi were lower in heavily disturbed soils than**
267 **historically disturbed and undisturbed soils ($P < 0.05$, One-way ANOVAs; Fig. 5a-f).** Similar to
268 the variation of fungi, the highest fungal: bacterial PLFAs (*c.* 0.35) were appeared in one of the
269 rangelands, and the lowest value occurred in rice field (*c.* 0.15) (Fig. 5g). Surprisingly, 17cy:
270 precursor (used as an indicator of the anaerobic stress) across 7 land use types fluctuated
271 disorderly at this regional scale (Fig. 5h).

272 Stepwise multiple regression analysis demonstrated that **54 % of the variation in microbial**
273 **community composition could be explained by soil moisture and tillage.** Soil moisture, soil total
274 **C content and radiative dry index together accounted for 32 % of the spatial variation in total**
275 **microbial biomass.** Soil moisture alone contributed to 57 % and 57 % of the variation in the
276 contributions of branched and monounsaturated PLFAs, respectively. In this region, radiative dry
277 index, soil **moisture and tillage** together accounted for **77 % and 65 %** of the variation in

278 contribution of fungal PLFAs and fungal: bacterial PLFAs. 38 % of the spatial variability in
279 contribution of bacterial PLFAs could be attributable to the combination of precipitation, soil
280 total C content, water holding capacity and tillage (Table 2).

281

282 **4 Discussion**

283 Exploring the primary drivers regulating distributions of soil microbial communities and teasing
284 apart relative contributions of multiple environmental factors (e.g. climate, soil texture, pH, soil
285 organic matter content, vegetation type), land management practices and spatial structure on
286 microbial community composition and biomass are important challenges in microbial ecology.

287 In this study, soil moisture is a main control on microbial communities across 7 land use types at
288 the regional scale, which explained 31 % of the variation in microbial community composition
289 (Fig. 4; Table 2). Multivariate analysis show that increased proportion of gram-positive bacteria

290 and decreased proportions of gram-negative bacteria and fungi were associated with sites with
291 higher water content (Fig. 5). These findings are in agreement with the previous observations

292 (Rinklebe and Langer, 2006; Entry et al., 2008; Clark et al., 2009; Drenovsky et al., 2010; Ma et
293 al., 2014). The stress of drought likely facilitates fungi to survive better, because soil fungi rely

294 on more aerobic conditions and are more tolerant to drought due to their filamentous nature

295 (Zhang et al., 2005a). The aerobic filamentous fungi have variable hyphal networks that can
296 relocate water and nutrient resource by cytoplasm translocation (Klein and Paschke, 2004).

297 Instead, the predominance of bacteria over fungi indicates adaptation of the soil microbial

298 communities to high water potential and limited aeration of the soils (Šantrůcková et al., 2003;

299 Drenovsky et al., 2004).

300 It has been proposed that the ratio of cyclopropane fatty acids to its precursor can be used to
301 indicate the levels of anaerobic and nutritional stress (Kieft et al., 1997; Drenovsky et al., 2010).
302 For instance, Drenovsky et al. (2010) have reported that cyclopropane fatty acid: precursor (17cy:
303 (16:1 ω 7c); 19cy: (18:1 ω 7c)) were significant high under conditions of low O₂ concentration and
304 high temperature. However, whether cyclopropane fatty acid is representative of aerobic
305 conditions is debatable. Bossio and Scow (1998) found that the cyclopropane fatty acids were
306 insensitive to water availability across a large-scale precipitation gradient in California. Similarly,
307 our result also show that the 17cy: precursor responded to high water availability modestly at
308 this region (Fig. 5h), whereas we do not know for sure what limits the cyclopropane formation.
309 This insensitivity to anaerobic conditions in the soils contrasts with its widespread use as an
310 anaerobic marker. These findings suggest that cyclopropane fatty acids to its precursor are not
311 generally useful as taxonomic indicators of respiratory type at large spatial scales.

312 [Distinct microbial community composition and biomass are associated with land disturbance](#)
313 [levels and management practices at the regional scale in northeast China](#). Continuously farmed
314 agriculture is widely occurring in various biomes across the world. Repeated tillage heavily
315 disturbs soil physical properties, and decreases soil bulk density and water retaining capacity
316 (Bescansa et al., 2006). This frequent disturbance in soil properties during tillage (and associated
317 fertilization) could rapidly alter microbial community composition due to different competitive
318 ability of specific microbial groups. The groups with the capacity of rapid adaptation to the
319 frequently changing soil environment (e.g. bacteria) could take advantage of new resources in

320 disturbed habitats (Cookson et al., 2008; Sun et al., 2011). Consistent with other large-scale
321 studies, conventional tillage soils had higher proportions of gram-positive bacteria, and had
322 lower proportions of fungi in this study (Fig. 2b) (Galvez et al., 2001; Zhang et al., 2005a). The
323 ability of gram-positive bacteria to sporulate may allow them with stand tillage or other
324 anthropogenic disturbance. In contrast, fungi are sensitive to disturbance and their hyphae
325 density would decrease significantly in response to tillage (Drenovsky et al., 2010).

326 Given the strong effects of heavy disturbance on soil microbial communities, it is interesting
327 to find that microbial community composition in lightly and historically disturbed soils (i.e.
328 grazed rangelands, returned croplands) were similar to those in undisturbed soils. These results
329 are supported by observations in other studies (Bardgett and McAlister, 1999; Ingram et al.,
330 2008; Sun et al. 2011). Ingram et al. (2008) reported that light grazing showed no effect on soil
331 C content and slightly increased gram-negative bacteria and fungi proportions. As the
332 disturbance ceased, microbial biomass increased, probably because more time and resources
333 were available for specific microbial groups which have slower growth rate (e.g. fungi) (Zhang
334 et al., 2005b). However, Buckley and Schmidt (2003) reported that microbial community
335 composition did not differ significantly between conventionally cultivated fields and fields that
336 had been abandoned from cultivation for nine years. A possible explanation of this result is that
337 long-term sustainable tillage altered soil physico-chemical structure and decreased nutrient
338 availability, thus the recovery of soil properties to pre-agricultural levels may require decades or
339 even centuries.

340 Many previous studies have demonstrated that vegetation types, soil properties and spatial

341 [structure can influence soil microbial community function and abundance](#) through providing
342 suitable habitats and food sources (Kourtev et al., 2003; Šantrůcková et al., 2003; Han et al.,
343 2007; [Chen et al., 2014](#)), whereas our findings of [microbial community composition were not](#)
344 [related to these factors across this region](#). In the current study, soils were sampled in different
345 vegetation types [and soil organic matter content](#), but the microbial community composition were
346 very similar at the same geographical location in natural habitats (e.g. meadow versus wood,
347 data not shown) (Fig. 5). Similar trends were observed in heavily disturbed habitats, the
348 distributions of microbial communities were depended on land disturbance [levels](#) and practices
349 rather than agricultural [plant species](#). For example, the farmland soils (e.g. corn, peanut, mung
350 bean, red bean) in the same location clustered together in CCA ordination despite the different
351 [plant species](#) that they represented (Fig. 2, 3, 5). These results were consistent with a recent
352 study, Drenovsky et al. (2010) reported that microbial community composition was more
353 strongly influenced by disturbance than by agricultural [plant species](#) in California.

354 Habitat factors and land management triggered complex interactive effects on soil microbial
355 community composition at the regional scale in northeastern China, as the value of shared
356 variance fraction was [15 %](#) without considering the variation explained by all three components
357 (Fig. 4). This was similar to the findings of Drenovsky et al. (2010) that environmental factors
358 caused significantly interactions on microbial community composition at large spatial and
359 temporal scales. The significant shared effects in our study could be attributed to the strong
360 effects of land [disturbance \(e.g. flooding, irrigation, tillage\)](#) on soil properties that then affect
361 microbial communities. The findings suggest that land management [could partly controlled soil](#)

362 [environmental effects on](#) microbial community composition and biomass at large spatial scales.

363 Inconsistent with the hypothesis, soil [moisture](#) and land use were the most important factors
364 driving microbial community composition and biomass at the regional scale in northeastern
365 China. In this study, soil [moisture](#) was determined not only by natural precipitation, but also by
366 managed inputs, thus the effect of precipitation was weaker but still significant. In addition,
367 factors such as spatial structure, soil texture, pH and vegetation types did not have significant
368 relationships with microbial community composition and biomass. These findings will improve
369 predictions of the ecological processes and consequences of ecosystems under global changes.

370

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375

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513

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	<i>n</i>
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
Chaghanhua	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
<i>Total</i>					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 r²	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

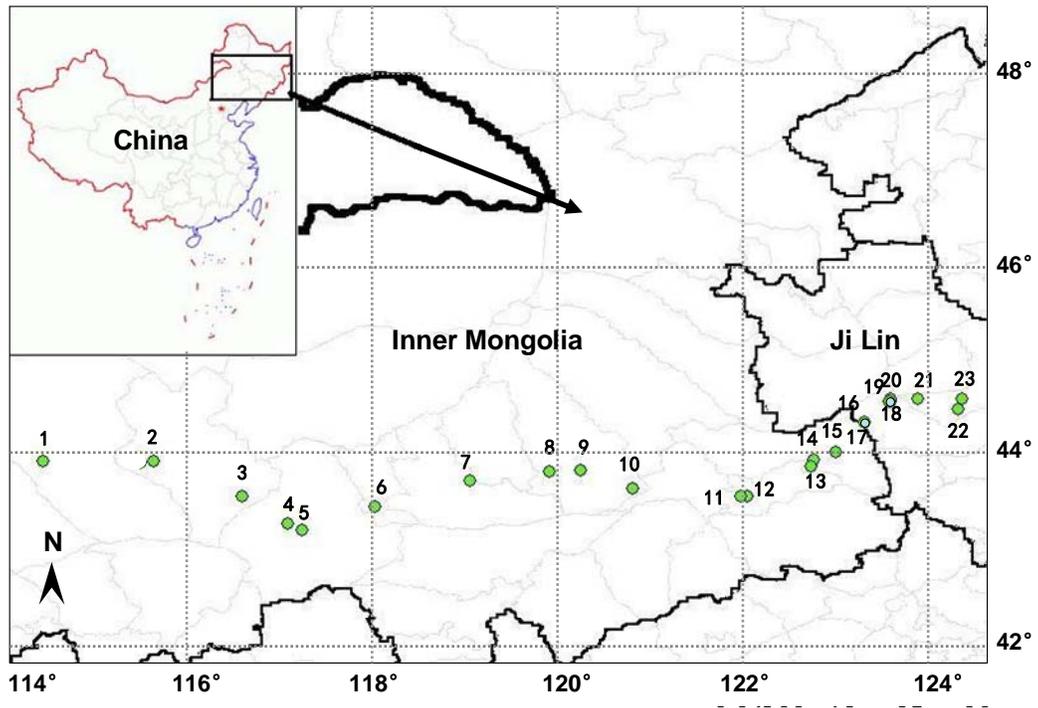


Fig. 2

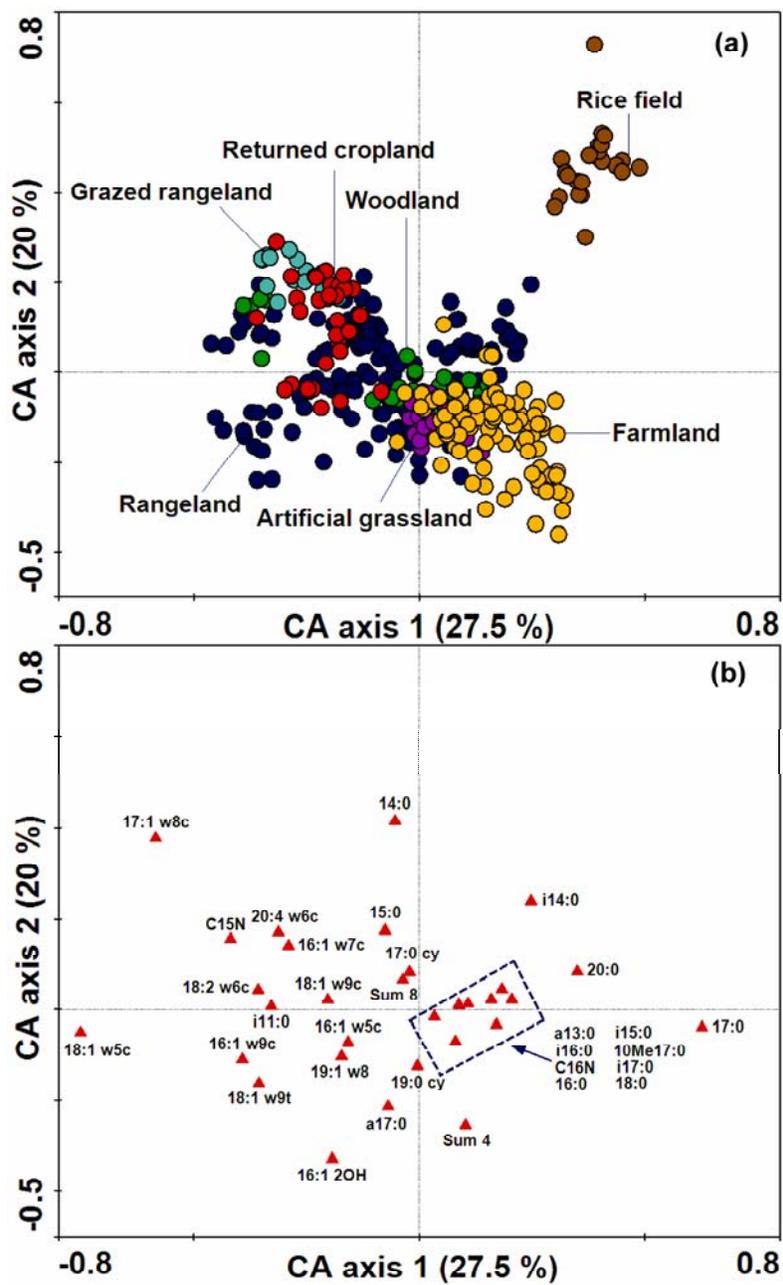


Fig. 3

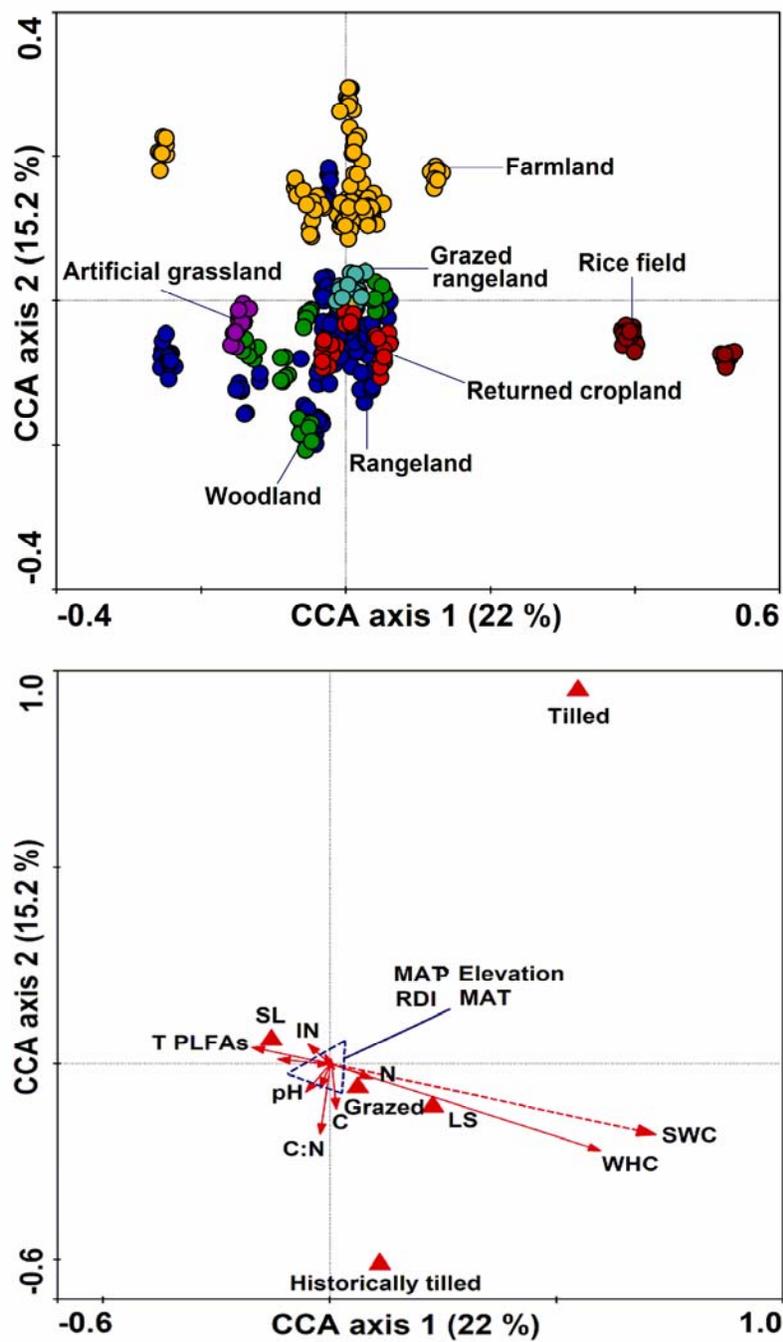


Fig. 4

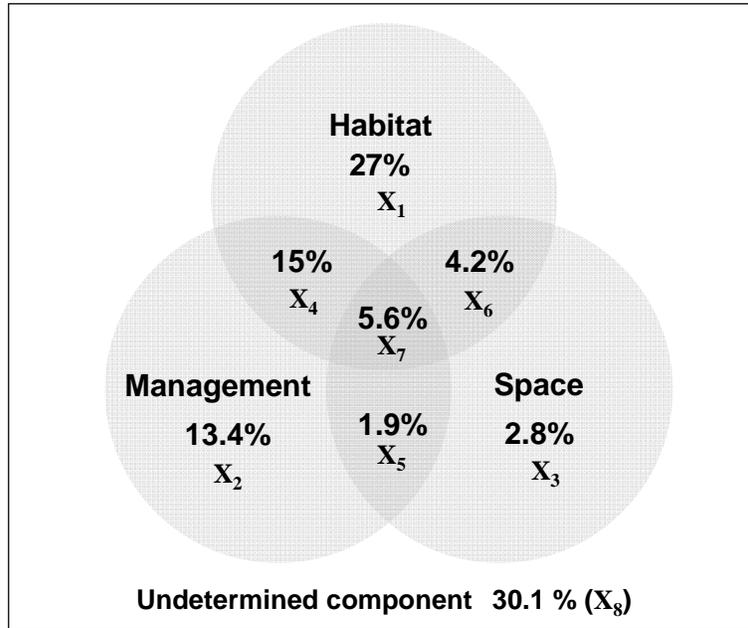
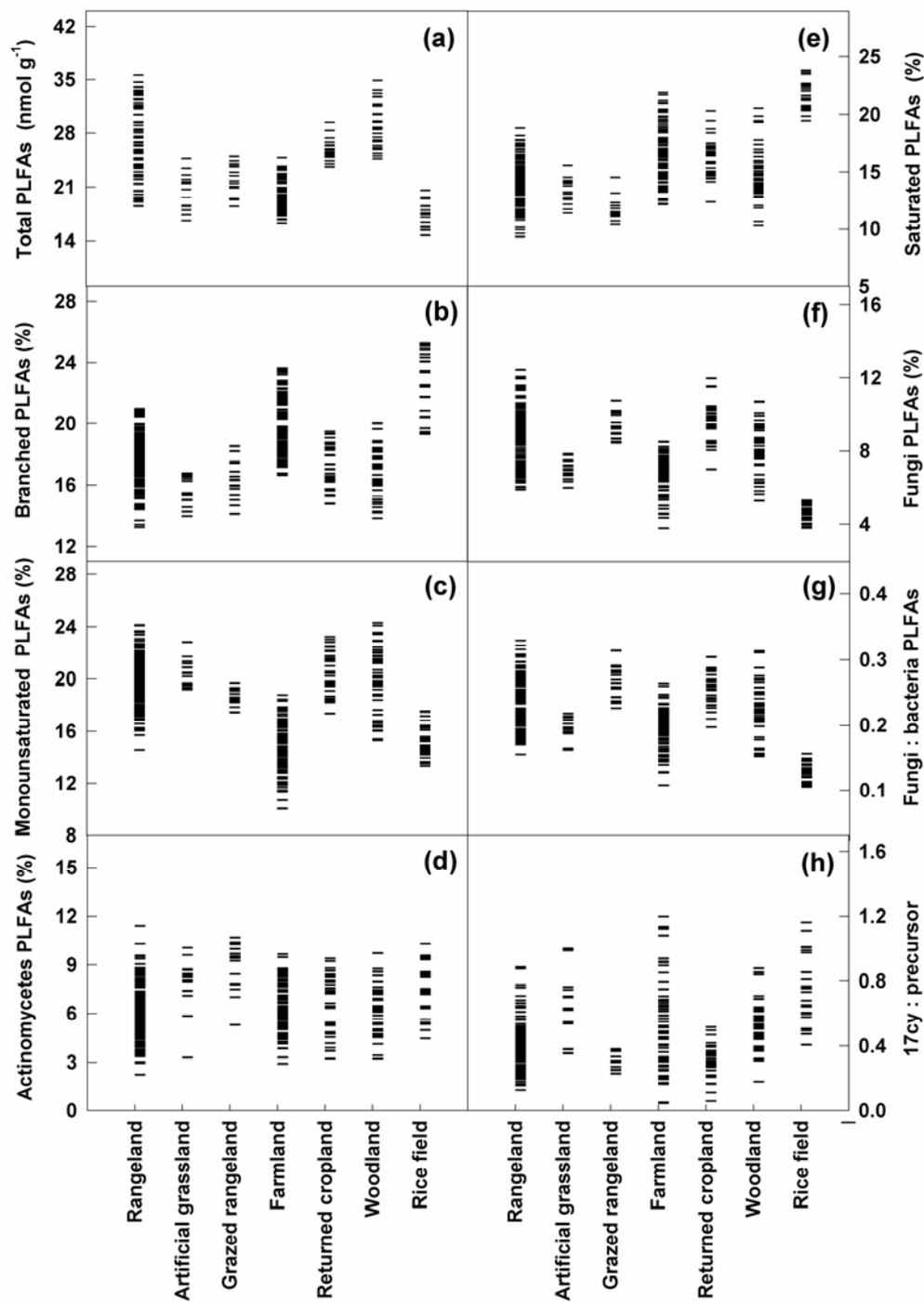


Fig. 5



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
Xinfuzhili	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
Molimiao	10	Farmland	Tilled	Corn	385	6.8	1.12	270	8.6	LS	0.9	0.11	8.08	11	24	20.80
	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