1 # Plant functional traits determine latitudinal variations
2 # in soil microbial function: evidence from forests in
3 # China
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28 **Abstract.** Plant functional traits have increasingly been studied as determinants of ecosystem
29 properties, especially for soil biogeochemical processes. While the relationships between biological
30 community structures and ecological functions are a central issue in ecological theory, these
31 relationships remain poorly understood at the large scale. We selected nine forests along the North–
32 South Transect of Eastern China (NSTEC) to determine how plant functional traits influence the
33 latitudinal pattern of soil microbial functions, and how soil microbial communities and functions are
34 linked at the regional scale. We found that there was considerable latitudinal variation in the profiles
35 of different substrate use along the NSTEC. Specifically, we found that the substrate use by
36 microorganisms was highest in the temperate forest soils (soil microbial substrate use intensities of
37 10–12), followed by the subtropical forest soils (soil microbial substrate use intensities of 7–10), and
38 was least in the coniferous forest soils (soil microbial substrate use intensities of 4–7). The latitudinal
39 variation in soil microbial function was more closely related to plant functional traits (leaf dry matter
40 content, leaf C concentrations, and leaf N concentrations, P=0.002) than climate (Mean annual
41 precipitation, P=0.022). The soil silt, leaf dry matter, and leaf C and N contents were the main
42 controls on the biogeographical patterns of microbial substrate use in these forest soils. The soil
43 microbial community structures and functions were significantly correlated along the NSTEC. Soil
44 carbohydrate and polymer substrate use were mainly related to soil G^+ bacterial and actinomycic
45 PLFAs, while the use of amine and miscellaneous substrates were related to soil G^- bacterial and
46 fungal PLFAs. The enzyme production varied with changes in the soil microbial communities. The
47 soil enzyme activities were positively correlated with the bacterial PLFAs but were not correlated
48 with the fungal PLFAs. The soil organic matter (SOM) decomposition rates were significantly higher
49 in the temperate forests than in the subtropical and tropical forests, emphasizing the rapid
50 degradability of high-energy substrates, such as soil microbial biomass carbon, carbohydrates, and
51 amino acids. The SOM decomposition rates were significantly and negatively related to soil dissolved
52 organic carbon concentrations, carboxylic acids, polymers, and miscellaneous substrate use. The
53 relationships between soil PLFAs and microbial substrate use, enzyme activities, and SOM
54 decomposition rate show that, as the soil microbial community structure changes, soil
55 biogeochemical processes also change.

56 **Abbreviations**

57 NSTEC North-South Transect of Eastern China
58 AWCD Average well color development
59 RDA Redundancy analysis

60 Soil microbial community

61 PLFAs Phospholipid fatty-acids
62 G^+ Gram positive bacteria
63 G^- Gram negative bacteria
64 F/B Fungi/Bacteria

65 Climate conditions

66 MAT: Mean annual temperature
67 MAP: Mean annual precipitation

68 Soil enzyme activities

69 BG β-glucosidase
70 NAG N-acetylglucosaminidase
71 AP Acid phosphatase
72 LAP Leucine aminopeptidase

73 Soil properties

74 SMC Soil moisture content
75 SOM Soil organic matter
76 SOC Soil organic carbon
77 TN Total Nitrogen
78 DOC Dissolved organic carbon
79 MBC Microbial biomass carbon
80 Silt Soil silt fractions (<53 μm)

81 Plant functional properties:

82 CWM Community-weighted means
83 SLA The specific leaf area
84 LDMC Leaf dry matter content
85 Leaf C Leaf C concentrations
86 Leaf N Leaf N concentrations

87 **1 Introduction**

88 The catabolic diversity of soil microbial communities is a useful indicator of how microbial functions
89 adapt to environmental stress. It can be used to test fundamental questions about soil biological
90 resistance and resilience (Jagadamma et al., 2014; Swallow and Quideau, 2015), and help us
91 understand the role of microbial communities in different environments (Preston-Mafham et al.,
92 2002). Biological community structure and function are intimately linked in ecological processes,
93 and their relationships are a central issue in ecological theory (Talbot et al., 2014). Therefore, a major
94 goal in ecological research is to identify and understand the mechanisms and relationships that control
95 the structure and function of microbial communities over large spatial scales.

96 Numerous studies have documented how environmental and anthropogenic perturbations
97 impact on the structure, diversity (Tu et al., 2016; Zhou et al., 2016), and enzyme activities (Peng
98 and Wang, 2016; Xu et al., 2017) of soil microbial communities, and have reported that forests in the
99 same climatic zone develop similar microbial communities. Other researchers have examined spatial
100 patterns in soil microbial function at different scales. For example, Tian et al. (2015), from their study
101 of Changbai Mountain, China, found that the soil microbial metabolic activity and functional
102 diversity were spatially dependent. Others reported that soil microbial activities varied by forest type,
103 with high local variation and significant separation along regional climate gradients (Brockett et al.,
104 2012; Cao et al., 2016). Soil microbes from different climatic zones have different affinities for
105 carbon substrates. For example, microorganisms from boreal pine forest soils used carboxylic acids
106 more efficiently, but decomposed amino acids much less efficiently, than microorganisms from
107 temperate forest soils (Klimek et al., 2016). The soil microbial metabolic abilities are also influenced
108 by the dominant tree species, through the production of chemically-unique litter and root exudates,
109 and the soil physico-chemical properties (Menyailo et al., 2002). Despite this, because of limitations
110 in analytical methods, questions still remain about how soil microbial functions vary at the regional
111 scale.

112 The functional diversity of soil microbial communities is regulated by physico-chemical soil
113 properties (Gartzia-Bengoetxea et al., 2016), climate (Cao et al., 2016), and the composition of plant
114 cover (Sherman and Steinberger, 2012). For example, the geographic patterns in soil microbial

115 activities mainly reflect the climate, soil pH, and total phosphorus concentrations over large
116 geographic scales (Cao et al., 2016). Research has shown that substrate-induced respiration rates
117 were higher in soil microbial communities that developed under beech and holm oak forests than
118 under oak and pine forests (Gartzia-Bengoetxea et al., 2016). Plant functional traits have increasingly
119 been studied as determinants of ecosystem properties, especially for soil biogeochemical processes
120 (De Vries et al., 2012; Pei et al., 2016). Soil bacteria phospholipid fatty-acids (PLFAs) were found
121 to be positively correlated with the community-weighted means (CWM) of plant functional traits
122 (leaf nitrogen (N) concentration) (De Vries et al., 2012). The plant leaf dry matter content and the
123 leaf carbon (C) to nitrogen (N) ratio both influence the multivariate soil microbial community
124 structure, and these factors positively promote the abundances of specific microbial functional groups
125 (Pei et al., 2016). Limited soil resources, particularly in tropical forests, mean that soil
126 microorganisms may be more reliant on plants than soil for C and nutrients via rhizosphere exudation
127 or litter production, which varies among plant species (Russell et al., 2007; Raich et al., 2014; Waring
128 et al., 2015). While soil functional diversity has been used as an indicator of microbial metabolic
129 potential, there have been few studies of the integrated effects of climate, vegetation, and soil
130 substrate availability on large-scale soil microbial functional diversity.

131 Although the functional characteristics of soil microorganisms are at least as important as their
132 patterns of community structure in biogeochemical studies, the links between microbial community
133 structure and microbial functions are poorly understood. There are two current hypotheses about how
134 microbes determine ecosystem process rates. In functional redundancy, different microbes perform
135 the same function and so changes in the microbial community structure do not necessarily lead to a
136 change in soil function (Balser and Firestone, 2005; Strickland et al., 2009). For example, Banerjee
137 et al. (2016) showed that the abundance of different bacterial and fungal groups changed by up to
138 300-fold under straw- and nutrient-amended treatments but that the decomposition rate remained
139 similar, indicating possible functional redundancy. The functional redundancy hypothesis has
140 recently been challenged by a counter-hypothesis, referred to as functional dissimilarity, which
141 suggests that diversity brings stability, and that every species plays a unique role in ecosystem
142 function (Fierer et al., 2007; Waldrop and Firestone, 2006). Soil microbial community composition
143 therefore, combined with environmental variables, may ultimately determine ecosystem process rates.

144 Waldrop and Firestone (2006) showed that gram positive bacteria (G^+) were mainly responsible for
145 the decomposition of pine needles and soil organic matter, but gram negative bacteria (G^-) were
146 mainly responsible for the decomposition of starch and xylose, which are easy to break down.
147 Philippot et al. (2013), when studying the diversity of denitrifiers, showed that the loss of microbial
148 diversity could result in decreases of between 4- and 5-fold in denitrification activity. In the
149 Mediterranean, losses in the mass of decomposing leaf litter from shrub species accelerated as
150 detritivore assemblages became more functionally dissimilar (Coulis et al., 2015). Research to date
151 suggests that the different microbial communities will result in variations in soil microbial function
152 and soil biochemical processes, so information about the relationships between soil microbial
153 communities and their functions in natural ecosystems is urgently needed.
154 The North-South Transect of Eastern China (NSTEC) extends from a cold temperate coniferous
155 forest in the north to a tropical rainforest in the south, and includes almost all the forest types found
156 in the Northern Hemisphere (Zhang and Yang, 1995) (Fig. 1 and Table 1). This transect, therefore,
157 provides the optimal environment for investigating large-scale geographical patterns in microbial
158 communities and their responses to environmental changes. In this study, we examined spatial
159 patterns in soil labile C concentrations, soil organic matter (SOM) decomposition rates, and
160 metabolic activity and functional diversity of microbes in nine forest biomes along the NSTEC. We
161 assessed how abiotic factors, such as climate, soil physical and chemical properties, and biotic factors,
162 in the form of community-weighted means (CWM) of plant functional traits, contributed to soil
163 functional diversity at the regional scale. We also examined the links between soil microbial
164 community structure (PLFAs) and function (SOM decomposition rate, enzyme activities, and
165 microbial substrate use). We tested four hypotheses in this study, as follows: (1) The profiles of soil
166 microbial substrate use vary along a latitudinal gradient, (2) biogeographical patterns of soil
167 microbial substrate use are constrained by climate and plant functional traits, and (3) different soil
168 microbial communities may have substrate use profiles and SOM decomposition rates.

169 **2 Material and methods**

170 2.1 Study area and soil sampling

171 We selected nine forest ecosystems along the NSTEC, namely Huzhong (HZ), Liangshui (LS),
172 Changbai (CB), Dongling (DL), Taiyue (TY), Shennong (SN), Jiulian (JL), Dinghu (DH), and
173 Jianfeng (JF) (18°44′–51°46′N, 128°53′–108°51′E) (Fig. 1, Table 1). Further information about the
174 soil types and sites has been documented previously by Xu et al. (2017). Forest soils have been
175 classified following the U.S. soil taxonomy and are described in Table 1 (Soil Survey Staff, 2010),
176 where information about the climate and the dominant vegetation at each site is also presented.

177 Soil samples were collected from four random plots at each site in July and August 2013, as
178 described previously by Xu et al. (2017). Briefly, we established four sampling plots measured 30 ×
179 40 m and collected soil samples from a depth of between 0 and 10 cm at between 30 and 50 points
180 in each plot along an S-shape. On return to the laboratory, the fresh soil samples were immediately
181 sieved through a 2-mm mesh and subdivided into three subsamples. One subsample was stored briefly
182 at 4 °C until analysis for soil enzyme activities and soil pH. Another was stored briefly at −20 °C
183 until analysis for PLFAs and Eco-Biolog. The third was air-dried, sieved through a 0.25 mm mesh,
184 and analyzed for soil nutrients.

185 2.2 Soil chemical analyses

186 Soil pH was measured at a soil-to-water ratio of 1:2.5. The soil moisture content (SMC) was
187 measured gravimetrically on 20 g fresh soil that was oven-dried at 105 °C to constant weight
188 immediately on arrival at the study sites' laboratories (Liu et al., 2012a). Soil organic carbon (SOC)
189 and total N (TN) concentrations were determined by dry combustion of ground samples (100-mesh)
190 in a C/N analyzer (Elementar, Vario Max CN, Germany). Total phosphorus (TP) was determined
191 with a flow injection auto-analyzer following digestion with H_2SO_4-$HClO_4$ (Huang et al., 2011).
192 After extraction with distilled water at a soil:distilled water ratio of 1:5, dissolved organic carbon
193 (DOC) concentrations were determined by Liqui TOC II (Elementar, Liqui TOC II, Germany) (Jones
194 and Willett, 2006). Soil microbial biomass carbon (MBC) was measured using the chloroform
195 fumigation and direct extraction technique (Vance et al., 1987). A conversion factor of 2.64 was used
196 to convert extracted C to biomass C. The silt fractions (<53 μm) of the samples were separated by
197 wet-sieving and then were freeze-dried in the laboratory, as described by Six et al. (2000). The soil
198 properties are shown in Table 2. We followed the method described by Bååth et al. (2003) for PLFA

199 analysis and PLFAs are expressed in units of nmol g^{-1}. The four enzymatic activities of β-glucosidase
200 (BG), N-acetylglucosaminidase (NAG), acid phosphatase (AP), and leucine aminopeptidase (LAP)
201 responsible for soil C, N, and phosphorous cycling, were measured following the procedure outlined
202 in Saiya-Cork et al. (2002) and are expressed in units of nmol h^{-1} g^{-1}. Information about PLFA and
203 enzyme activities are presented in Table S1.
204 The Biolog-ECO plates were purchased from Biolog, US. The substrates for BG, NAG, AP, and
205 LAP were 4-MUB-β-D-glucoside, 4-MUB-N-acetyl-b-D-glucosaminide, 4-MUB-phosphate, and L-
206 Leucine-7-amino-4-methylcoumarin, and were stored at −20 °C. An MUB standard was used for the
207 BG, NAG, and AP enzymes and an AMC standard was used for the LAP enzyme. The substrates and
208 standards were purchased Sigma. Analytical grade reagents were used for the soil nutrient analysis.

209 2.3 Vegetation data

210 We established four sampling plots (30×40 m) in each forest ecosystem. In each plot, we recorded all
211 the tree individuals, and measured the height and diameter-at-breast-height (DBH) of each woody
212 individual with a DBH≥2 cm. The diversity of the tree species in the sampling plots was represented
213 by H′, and the diversity (H′, Shannon-Wiener) of the tree species in the community was calculated
214 as follows:

215 $$H' = \sum_{i=0}^{n} (PilnPi)$$

216 Where P_i was the importance value of the species *i* as a proportion of all species, and *n* was the
217 number of the species.
218 We also calculated the community-weighted means (CWM) values of the tree traits using the
219 cover of each tree. As described by Xu et al. (2018), we collected litter and sun-exposed and mature
220 leaves (leaf blades for trees) from between five and ten individuals of each plant species at each site
221 and determined their TN and TC concentrations. We calculated the specific leaf area (SLA, the one-
222 sided area of a fresh leaf divided by its oven-dried mass, m^2 kg^{-1}), leaf dry matter content (LDMC,
223 the oven-dried mass of a leaf divided by its water-saturated fresh mass, mg g^{-1}), leaf C concentrations
224 (leaf C, g kg^{-1}), and leaf N concentrations (leaf N, g kg^{-1}) for ten fully expanded leaves of each
225 sampled individual. To measure the leaf traits at the community level, we calculated the CWM of the

226 tree layer, as follows:

227 $$\mathrm{CWM} = \sum_{i=1}^{n} pi \times \mathrm{trait}_i$$

228 Where *pi* is the relative contribution of the species *i* to the cover of the whole community, *n* is the
229 number of the most abundant species, and trait $_i$ is the trait value of species *i*, as described by Garnier
230 *et al*. (2004). The diversity of the tree species and plant functional traits are summarized in Table S2.

231 2.4 Microbial substrate use

232 Microbial functional diversities were determined using a Biolog EcoPlate™ (Biolog Inc., Hayward,
233 California, USA) as described by Garland and Mills (1991). Briefly, approximately 10 g of fresh soil
234 was suspended in 100 ml saline solution (0.85% NaCl) and shaken on an orbital shaker for 30 min at
235 190 rpm. A 150 μl aliquot of supernatant from 1:1 000 dilutions of each soil sample was added to
236 each well. The plates were incubated at 25°C, and the absorbance at 590 nm was measured using a
237 microplate reader (GENios Pro™, Tecan Trading AG, Männedorf, Switzerland) every 24 h up to 240
238 h (0, 24, 48, 72, 96, 20, 144, 168, 192, 216, and 240 h). To minimize the influence of cell density in
239 comparisons among samples, results can be analyzed at constant average well color development
240 (AWCD). The AWCD for each microplate was calculated by subtracting the control well optical
241 density (OD) from the substrate well OD (blanked substrate wells), setting any resultant blanked
242 substrate wells with negative values to 0 and taking the mean of the 95 blanked substrate wells.

243 The Richness (*R*), Shannon-Weiner diversity index (*H'*), Shannon evenness index (*E*), and
244 Simpson dominance index (*D*) were calculated from the absorption values after EcoPlate™
245 incubation for 96 h (Gomez et al., 2006). Additionally, the 31 C sources were divided into six groups,
246 namely carbohydrates, carboxylic acids, amines, amino acids, polymers, and miscellaneous, as
247 suggested by Zak et al. (1994). The average absorbance of all C sources within each group was
248 computed as the intensity of the single substrate use. The soil total microbial metabolic intensities (*S*)
249 of six carbon sources were estimated by the area underneath *AWCD* vs. *t*, and were obtained by
250 integrating the equation against time t (Guckert et al., 1996):

251 $$\boldsymbol{S} = \sum [(\boldsymbol{v_i} + \boldsymbol{v_{i-1}})/\mathbf{2} \times (\boldsymbol{t_i} + \boldsymbol{t_{i-1}})]$$

252 Where v_i was the average optical density of the *i*th incubation time.

253 2.5 SOM decomposition rate

254 Four replicates from each sampling site with a 60% water-holding capacity were incubated at 20°C.
255 In brief, 40 g of each fresh soil sample were put into a 150-ml incubation bottle, and the samples
256 were then adjusted so that their moisture content corresponded to a water-holding capacity of 60%.
257 During the 4-week incubation period, the soil respiration rates were measured on days 1, 7, 14, 21,
258 and 28 using an automatic system. The SOM decomposition rates were calculated as described in the
259 study of Xu et al. (2015).

260 2.6 Statistical analysis

261 One-way analysis of variance (ANOVA) followed by a post hoc Tukey HSD test were used to test
262 the significance of the differences among the soil properties, C use, functional diversity, and SOM
263 decomposition rates in the different forest ecosystems. We tested the relationships between labile C,
264 soil microbial community structure, microbial function, and the SOM decomposition rates with the
265 Pearson correlation test. Differences were considered significant when $P<0.05$, with the marginal
266 significance set at $P<0.01$. All P values were adjusted using the Bonferroni correction to account for
267 multiple comparisons.

268 We used redundancy analysis (RDA) to examine the relationship between the environmental
269 variables and soil microbial substrate use. The environmental variables were the same as those
270 described in Xu et al. (2018), including climate, soil properties, litter properties, and plant functional
271 traits. Before RDA, we conducted forward selection of the environmental variables that were
272 significantly correlated with variations in the microbial substrate use profile using stepwise
273 regression and the Monte Carlo Permutation Test. We used CANOCO software 4.5 (Ter Braak and
274 Smilauer 2002) for the RDA and stepwise regression. The environmental properties, which were
275 significantly correlated with the microbial substrate use in the RDA, were stressed in the plots. Path
276 analysis was conducted to examine the direct and indirect effect of biotic and abiotic factors on soil
277 microbial use of carbon sources. All ANOVA, regression analyses, and path analysis were performed
278 using SPSS 19.0 for Windows. Data are reported as the mean ± SE.

279 **3 Results**

280 3.1 Patterns in the microbial substrate use, soil labile carbon, and SOM decomposition rates

281 There was no obvious latitudinal pattern for the soil total microbial metabolic intensity (Fig.2). Of
282 the forests along the NSTEC, the C metabolic intensity of soil microbes was lowest in HZ and LS;
283 the C metabolic intensity of soil microbes differed significantly between JF and the other forests (Fig.
284 2), which indicates that the color development was significantly higher in the tropical forest soils
285 than in the subtropical and temperate forest soils and is consistent with the variations in the AWCD
286 (Fig. S1). The average values of R, H', and D were significantly different among the nine forest soils
287 and were highest in JF, SN, and CB (Table 3). Generally, the soil microbial use of the six different
288 carbon sources were relatively higher in tropical and subtropical climatic area (low latitude) than
289 those in temperate climatic area (high latitude) (Fig.3).

290 Across the nine forests, soil microorganisms used the six substrate groups in the same order; the
291 carboxylic acid substrate was used most, followed by amino acids, carbohydrates, polymers, amines,
292 and miscellaneous substrates (Fig. 3). Microorganisms in the boreal and temperate forests mainly
293 metabolized carbohydrates, amino acids, and carboxylic acids, while those from the subtropical and
294 tropical forests used the substrates in equal proportions. The substrate microbial use ability was
295 highest in the coniferous broad-leaved mixed forest and tropical forest soils, and lowest in the
296 coniferous forest soil (Fig. 3).

297 Overall, soil MBC concentrations in the boreal and temperate forests were three to eight times
298 higher than those of the subtropical and tropical forests. In contrast, the average DOC concentrations
299 in the tropical and subtropical forest soils, which ranged from 311 to 458 mg kg^{-1}, were significantly
300 higher than the average concentrations in the temperate and boreal forest soils, where the average
301 concentrations ranged from 204 to 284 mg kg^{-1} (Table 2). The average SOM decomposition rates in
302 the subtropical forests ranged from 0.64 to 2.42 μg C g^{-1} d^{-1}, and were significantly lower than the
303 rates in the temperate forests, which ranged from 3.43 to 4.61 μg C g^{-1} d^{-1} (Table S3).

304 3.2 Effect of environmental properties on soil microbial substrate use

305 Redundancy analysis showed that the variations in soil microbial substrate use were strongly and
306 positively correlated with the CWM values of LDMC, leaf N, and leaf C, and strongly and negatively

307 correlated with the soil silt content and SMC (Fig. 4). The RDA2 of soil microbial substrate use was
308 strongly positively correlated with TN and SOC, but negatively correlated with the mean annual
309 precipitation (MAP) (Fig. 5). RDA1 mainly represented the plant functional traits, soil texture, and
310 micro-meteorological conditions, while RDA2 represented climate and soil nutrients. Overall, the
311 soil silt content and the CWM values of plant functional traits were the main predictors of the
312 latitudinal variation in the soil microbial substrate use along the NSTEC.

313 3.3 Relationships between soil microbial substrate use, enzyme activities, and PLFAs

314 Microbial carbohydrate use was positively related with bacterial biomass and actinomycic biomass
315 (Fig. 5). Microbial polymer use was negatively related with bacterial biomass and actinomycic
316 biomass. Microbial amines use was negatively related with G^{-} bacterial and fungal biomass.
317 Miscellaneous substrate use was positively related with fungal biomass and G^{+}/G^{-} bacterial biomass
318 (Fig. 5).

319 The abundance of G^{-} bacteria was positively associated first with the specific activities of BG,
320 whereas actinomycetes and G^{+} bacteria were positively associated with BG and LAP. Soil fungi were
321 negatively associated with BG (Fig. 5).

322 3.4 Relationships between SOM decomposition rate, PLFAs, enzyme activity, and microbial
323 metabolic activities

324 The SOM decomposition rates were significantly and positively related to soil MBC concentrations
325 but significantly and negatively related to soil DOC concentrations (Fig. 6a and b). Except for amino
326 acid and amine substrates, the SOM decomposition rates were significantly and positively related to
327 microbial metabolic activities (AWCD) and carbohydrate substrate use (Fig. 6c and d) and negatively
328 related to carboxylic acid, polymer, and miscellaneous substrate use (Fig. 6e, g, and i).

329 The SOM decomposition rates were significantly and positively correlated with total PLFAs
330 (r=0.456, P=0.005), bacteria (r=0.3836, P=0.021), actinomycetes (r=0.500, P=0.002), and G^{-}
331 bacteria PLFAs (r=0.520, P=0.001) (Fig. 7a, b, d, and f) but were negatively correlated with fungal
332 PLFAs (r=−0.370, P=0.026), F/B (r=−0.513, P=0.001), and the G^{+}/G^{-} (r=−0.496, P=0.002) (Fig. 7c,
333 g, and h). Except for LAP activity, soil enzyme activities were significantly and positively correlated

334 with the SOM decomposition rates (P<0.01) (Fig. 7i, j, and l).

335 4 Discussion

336 4.1 Response of soil labile C and SOM decomposition rates to variations in forest type

337 Soil organic matter is one of the most important C pools in terrestrial ecosystems. The concentrations
338 of soil DOC in the temperate forests were lower than those in subtropical forests but the soil MBC
339 concentrations were higher in temperate forests than in subtropical forests. This reflects the results
340 of previous regional and global studies (Tian et al., 2010; Xu et al., 2013), and shows that the
341 production/consumption ratio of soil DOC was lower, but that microbial C immobilization was higher,
342 in the high latitude forests than closer to the tropics (Fang et al., 2014). Soil DOC, as a labile SOM
343 fraction with a rapid turnover, is one of the primary energy sources for microorganisms. The higher
344 temperatures and precipitation in subtropical and tropical forests lead to higher turnover rates (Fang
345 et al., 2014), so soil DOC concentrations were highest in subtropical, and MBC concentrations were
346 lowest, in tropical forests. However, in temperate forests, more C is assimilated into microbial
347 biomass, so that less C is lost through chemical and physical processes (Liu et al., 2010). Also,
348 because the decomposition ability of different microbe groups varies, the differences in the soil
349 microbial communities in different forest ecosystems may also be responsible for the spatial
350 variations in the soil DOC and MBC concentrations along the NSTEC (Hagedorn et al., 2008).

351 Heterotrophic soil respiration is sustained by the decomposition of SOM. The SOM
352 decomposition rates along the NSTEC were greater in temperate forests than in subtropical forests,
353 which was consistent with the variations in the soil MBC and SOC concentrations. These results
354 indicate that, as found in other studies, large scale SOM decomposition rates are driven by the
355 amounts of substrate available (Yu et al., 2010). Changes in the availability of C in SOM may affect
356 the microbial resource strategies, which may in turn influence the SOM decomposition rate. Some
357 forest soils were intermittently saturated (such as CB, Table 2) or high with mean annual precipitation.
358 Under the anaerobic conditions, soil organic decomposition is mediated by a complex suite of
359 microbial processes (Megonigal et al., 2004). The fermentation products including low molecular
360 weight alcohols, fatty acids, and dihydrogen can serve as substrates for anaerobic respiration using a

361 variety of alternative terminal electron acceptors in place of oxygen to mineralize organic carbon to
362 carbon dioxide (CO2). Therefore, the soil organic matter decomposition rate might be slow in these
363 anaerobic conditions. These results demonstrate that the reduction of organic matter is a key step of
364 anaerobic decomposition (Keller and Takagi, 2013).

365 4.2 Mechanisms driving latitudinal variations in microbial substrate use

366 The AWCD reflects the sole C source use ability of the soil microbial community (Garland and Mills,
367 1991). Of the six groups of C substrates, microbial communities in the temperate forests mainly used
368 carbohydrates, carboxylic acids, and amino acids, which suggests that microorganisms in temperate
369 forests probably use high-energy substrates that degrade easily (Kunito et al., 2009). The carbon
370 substrate use was lowest in the boreal coniferous forest (HZ). This shows that, compared with
371 coniferous species, broadleaved tree species produce root exudates and litter high in water-soluble
372 sugars, organic acids, and amino acids that are more favorable for microbial activity (Priha et al.
373 2001).

374 There was no significant latitudinal pattern in the soil total microbial metabolic intensity (S) in
375 our study, which was inconsistent with hypothesis (1). However, there was significant latitudinal
376 variation in the use of the six different carbon sources. The soil microbial use of carbon sources were
377 relatively higher in tropical and subtropical climatic area than those in temperate climatic area.
378 Consistent with hypothesis (2), soil microbial functions were similar in closely related to the CWM
379 values of the tree species (Fig. 4). However, only MAP of climatic factors had a moderate effect on
380 the soil microbial function (Fig. 4). Climate may have indirect effect on the latitudinal pattern of
381 different carbon sources use. In our study, MAT and MAP affected the six different carbon sources
382 use indirectly by influencing the soil temperature (ST), soil total nitrogen (TN), and total phosphorus
383 (TP) (Table S4-9). It was reported that climate was the main environmental parameters driving the
384 latitudinal patterns of community-level leaf traits through the regulation of species composition
385 (Wang et al., 2016). Woody plant species with evergreen broadleaves dominated in the tropic regions
386 characterized by hot, humid, and infertile habitats showed low CWM values of leaf N and SLA and
387 high CWM values of LDMC (Table S2).

388 A growing number of studies reported that vegetation type, land use, soil nutrients, and soil

389 organic matter quality and quantity can determine large scale patterns of microbial communities (de
390 Vries et al., 2012; Tu et al., 2016). Plant functional traits that are related to growth may determine a
391 tree species' ability to contribute to the soil carbon pool via leaf litter inputs. For example, it was
392 previously reported that plant traits such as the leaf N content, SLA, and LDMC could explain
393 variations in soil nutrients and litter decomposition rates (Eichenberg et al., 2014; Laughlin, 2011).
394 Therefore, we examined how these plant traits influenced the soil microbial function by latitude. We
395 found that changes in the soil microbial C substrate use with latitude were mainly related to the soil
396 silt contents and the CWMs of LDMC, and leaf C and leaf N concentrations, which indicates that the
397 quality of nutrients from plants had a major influence on microbial carbon use efficiency (Hypothesis
398 (2)). Plant species with high a SLA, high leaf N concentrations, and low LDMC can produce
399 bacterial-dominated soil microbial communities in grasslands (Orwin et al., 2010). Looking beyond
400 individual traits, related tree species may cultivate microbial communities with similar preferences
401 for carbon sources through coevolution of plants and microbes (Liu et al., 2012b; Buscot, 2015).

402 As hypothesized, the soil microbial community composition was explained by the CWMs of
403 plant traits at the regional scale. Carbon substrate use was negatively correlated with the CWM of
404 leaf N concentrations (Table S2, Fig. S2). Bacterially dominated soil microbial communities develop
405 from leaf litter comprised of N-rich leaves from fast growing species (De Vries et al., 2012), while
406 leaves with low N concentrations will promote fungal domination (Orwin et al., 2010; De Vries et
407 al., 2012). In line with this, fungal biomass decreased, and bacterial biomass increased, as the CWM
408 leaf N content increased, and is associated with fast-growing, N-exploitative plants (Xu et al., 2018).
409 Leaf N concentrations are considered as indicators of plant growth and resource uptake (Wright et
410 al., 2004). The results from this study show that, along the NSTEC, high leaf N restrained microbial
411 C substrate use (Fig.S2) and was a good indicator of the competition between plants for soil N (Pei
412 et al., 2016). Soil microbes and nearby plants may have been competing for N in the soil.

413 We also found that the C substrate use was negatively correlated with the CWM of leaf C
414 concentrations (Table S2, Fig. S2). Plants at high latitudes may have higher leaf C concentrations
415 than plants at lower latitudes so that they can balance the osmotic pressure of cells and resist freezing
416 (Millard et al., 2007; Hoch and Körner, 2012). The increased C was most likely in the form of an
417 increase in non-structural C, including starch, low molecular weight sugars, and storage lipids that

418 are easy to break down. Therefore, soil microorganisms from the temperate forests mainly
419 metabolized high-energy substrates, such as carbohydrates, carboxylic acids, and amino acids.

420 The LDMC is the ratio of the leaf dry weight to the fresh weight and has been used as a proxy
421 for the ratio of structural compounds to assimilatory tissue (mesophyll and epidermis, Van Arendonk
422 and Poorter, 1994). High values of LDMC indicate large amounts of vascular tissue, cellulose,
423 insoluble sugars, and leaf lignin that are difficult to decompose (Poorter and Bergkotte, 1992); C
424 substrates such as carbohydrates, carboxylic acid, and amino acid are, however, easy to decompose
425 (Myers et al., 2001). In line with this, the use of carbohydrate, carboxylic acid, and amino acid
426 substrates was negatively related to the CWMs of the LDMC (Table S2). Pei et al. (2016) reported
427 that the LDMC was an important driver of multivariate soil microbial community structure and G^{-}
428 bacterial abundance.

429 Soil texture regulates soil biological processes and so affects the soil microbial community
430 structure (Sessitsch et al., 2001). In the present study, microbial C substrate use was significantly and
431 positively related to the soil silt content. Soil types and textures varied along the NSTEC. Soil texture
432 influences how microbes use organic matter, and has a strong influence on soil moisture, nutrient
433 availability, and retention (Veen and Kuikman, 1990). Fine-textured soils with a higher silt content
434 are known to be more favorable for bacterial growth than soils with a lower silt content because of
435 their greater water-holding capacity and nutrient availability, and because they are better protected
436 from bacterial grazers (Carson et al., 2010). We found that the microbial C substrate use was higher
437 in LS, CB, SN, and JL than in the other forests, reflecting their fine-grained soils and high silt contents,
438 which ranged from 60% to 80%.

439 4.3 Links between soil microbial community structure and function

440 The soil microbial community structure and functions were significantly correlated along the NSTEC.
441 Soil carbohydrate and polymer substrate use were mainly related to soil G^{+} bacterial and actinomycic
442 biomass, but amines and miscellaneous substrates were mainly related to soil G^{-} bacterial, fungal
443 biomass, and the F/B ratio. Soil bacteria mainly decomposed simple carbohydrates, organic acids,
444 and amino acids, whereas soil fungi mainly decomposed recalcitrant compounds (Myers et al., 2001;
445 Treonis et al., 2004). Consistent with this, soil bacterial PLFAs were positively correlated with the

446 carbohydrate substrate use and the fungal PLFAs were positively related with miscellaneous substrate
447 use. The results are similar to those reported by Sterner and Elser (2002), who found that fungi tended
448 to have higher C/N or C/P ratios while heterotrophic bacteria typically have lower C/N or C/P ratios.
449 Shifts in microbial community composition may influence enzyme production (DeForest et al.,
450 2012; Waldrop et al., 2000; Brockett et al., 2012). Different microbial groups require different
451 amounts of nutrients to construct biomass, or have enzymes that differ in their affinity for nutrients.
452 We found that the relative abundances of the G^+ bacteria and actinomycetes communities were
453 associated with the specific activities of BG, AP, and LAP), whereas the relative abundance of the
454 G^- bacteria was correlated with soil NAG activities involved in chitin degradation. In agreement with
455 our study, numerous other researchers have reported significant correlations between PLFA profiles
456 and enzyme activities (Waldrop et al., 2000; DeForest et al., 2012; Brockett et al., 2012; Riah-Anglet
457 et al., 2015). Soil BG was mainly responsible for cellulose degradation and was involved in breaking
458 down complex organic compounds (cellobiose) into small molecule substrates (glucose) in favor of
459 acquiring C through microbial community growth (Waldrop et al., 2000). Soil NAG activities were
460 weakly and positively related with fungal biomass in the present study, and may have been mainly
461 produced by fungal populations (Valášková et al., 2007). Fungi are commonly considered as
462 producers of oxidative enzymes. Therefore, the influence of fungal biomass on variations in enzyme
463 activities was minimal (Kivlin and Treseder, 2014). The linkages between enzyme activity and
464 community composition may provide some insight into the microbial mechanisms that drive the
465 decomposition of macromolecular C compounds. These results suggest that that overall ecosystem
466 functioning may suffer if soil microbial groups are lost.
467 The quality and amounts of SOM are influenced by the biomass, vegetation coverage, root
468 distribution, and microbial species (Raich and Schlesinger, 1992). The SOM decomposition rates
469 were higher in temperate forests than in tropical forests and may reflect the higher soil microbial
470 biomass (Wang et al., 2016). In line with this, SOM decomposition rates were positively related with
471 soil MBC concentrations and different groups of PLFAs. The inverse relationships between SOM
472 decomposition rates and DOC, carboxylic acids, polymers, and miscellaneous along the NSTEC,
473 indicate a shift in the soil C turnover from open to closed with increases in the soil labile C
474 concentrations (Fang et al., 2014). Soil DOC and MBC influence SOM decomposition rates indirectly

475 by regulating microbial properties (Boberg et al., 2014; Wei et al., 2014). In our study, SOM
476 decomposition rates were positively related with bacterial PLFAs but negatively with fungal PLFAs.
477 Because different communities of microbes have different SOM use efficiencies (Balser and Wixon,
478 2009; Lipson et al., 2009; Monson et al., 2006), changes in the microbial community structure may
479 influence the microbial activities and the decomposition rates of organic matter (Lipson et al., 2009;
480 Keiblinger et al., 2010). The functional dissimilarity of microbes and fungi may help explain these
481 results. However, we did not measure some key variables, such as the microbial competition and
482 interactions, and relationship between the microbial diversity and the decomposition rates. Therefore,
483 in the future, we will use different experimental techniques that will help us gain an improved
484 understanding of the mechanisms that drive the relationships between the structure and function of
485 microbial communities.

486 **5 Conclusions**

487 In this study, we examined the patterns in labile C concentrations, SOM decomposition rates,
488 microbial substrate use, and functional diversity and identified a combination of abiotic and biotic
489 factors that influenced soil microbial functional diversity at the regional scale. The MBC
490 concentration and SOM decomposition rates were significantly lower, and the soil DOC
491 concentrations were higher in the subtropical and tropical forests than in the temperate forests. There
492 was no obvious latitudinal pattern for the soil total microbial metabolic intensity. However, soil
493 microbial use of the different carbon sources varied with the latitude except the amines carbon source.
494 Soil microbial use of carbon sources were relatively higher in tropical climatic areas. For the first
495 time, we showed that CWM values of plant traits explained variations in soil microbial C substrate
496 use at the regional scale. Additionally, the fine-grained soils with high silt contents were higher in
497 the microbial C substrate use. Climate factors affected the soil microbial uses of carbon sources
498 indirectly by influencing the soil temperature (ST) and soil nutrition. Soil microbial community
499 structure and function were strongly related, which suggests that the loss of soil microbial groups
500 may have consequences for overall ecosystem functioning.

501 *Data accessibility*. Requests for data and materials should be addressed to N.H. (henp@igsnrr.ac.cn) and G.Y.
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705 # Figures legends

706 **Fig. 1.** Distribution of typical forest ecosystems along the North-South Transect of eastern China (NSTEC). The
707 abbreviations for the sampling sites from north to south are as follows: HZ, Huzhong; LS, Liangshui; CB, Changbai;
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709 the nine forests throughout.
710 **Fig.2.** Variations in soil microbial substrate use during a 240-h incubation for the nine forests. Different colors
711 represent different forest types: Yellow, coniferous forest; Dark yellow, coniferous broad-leaved mixed forest; Purple,
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715 **Fig. 3.** Characteristics of microbial use of (a) carbohydrates, (b) carboxylic acids, (c) amino acids, (d) polymers, (e)
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717 **Fig.4.** Redundancy analysis (RDA) ordination biplot of soil microbial carbon sources use efficiency and
718 environmental properties. The representatives of different colors were showed in Figure 2. The dotted lines and solid
719 lines represent the environmental variables and lipid signatures and carbon sources. The abbreviations of the variables
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721 Leaf C, leaf carbon content; Leaf N, leaf nitrogen content; SLA, specific leaf area. Soil properties included SMC, soil
722 moisture content; Silt, soil silt content; TN, soil total nitrogen; SOC, soil organic carbon. The abbreviations of the
723 sampling sites were given in Table 1
724 **Fig.5.** The heatmap of the Pearson's correlation coefficients between the use of individual substrates and microbial
725 PLFAs and soil enzyme activities. Note: The abbreviations of the variables: Actino-, actinomycetes; F/B,
726 fungi/bacteria; G^+, gram positive bacteria; G^-, gram negative bacteria; G^+/G^-, Gram-positive bacteria/ Gram-negative
727 bacteria. BG, β-1, 4-glucosidase; NAG, β-1,4-N-acetylglucosaminidase; LAP, leucine aminopeptidase; AP, acid
728 phosphatase. $^{**}P< 0.01$, $^{*}P< 0.05$.
729 **Fig. 6.** Relationships between soil carbon mineralization rates (μg C $g^{-1}d^{-1}$) and microbial biomass C (MBC), soil
730 dissolved organic C (DOC), average well color development (AWCD), and individual substrate use.
731 **Fig. 7.** Relationships between soil carbon mineralization rates (μg C g^{-1} d^{-1}) and different groups of soil microbial
732 PLFAs (a-h) and enzyme activities (i-l).
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734

735 # Supporting information

736 **Table S1** Average values of forest soil enzyme activities and different PLFA groups along the NSTEC.
737 **Table S2** Plant diversity and community weighted means of plant functional traits
738 **Table S3** Soil organic matter (SOM) decomposition rates during the28 days of incubation time (Mean±SE) (μg C
739 g^{-1} d^{-1})
740 **Table S4** Path analysis of environmental variables to soil microbial use of carbohydrates source
741 **Table S5** Path analysis of relevant environmental variables to soil microbial use of carboxylic acids source
742 **Table S6** Path analysis of relevant environmental variables to soil microbial use of amino acids source
743 **Table S7** Path analysis of relevant environmental variables to soil microbial use of polymers source
744 **Table S8** Path analysis of relevant environmental variables to soil microbial use of amines source
745 **Table S9** Path analysis of relevant environmental variables to soil microbial use of miscellaneous source
746 **Fig. S1** Variations in the average well color development (AWCD) values during a 240-h incubation for the nine
747 forests. The abbreviations of the sampling sites are the same as those in Table 1.
748 **Fig.S2** The Pearson's correlation coefficients between the use of individual substrates and plant functional traits.

749 **Tables**

750 **Table 1.** The main characteristics of the sampling sites along the North South Transect of East China

Sampling Sites	Longitude (E)	Latitude (N)	Elevation (m)	MAT[b] (℃)	MAP[b] (mm)	Vegetation types	Soil type
HZ[a]	123°01′12″	51°46′48″	850	−3.7	473	Cold temperate coniferous forest	Spodosols
LS	128°53′51″	47°11′06″	401	0.01	648	Temperate conifer broad-leaved mixed forest	Albi-Boric Argosols
CB	128°05′27″	42°24′16″	758	2.8	691	Temperate conifer broad-leaved mixed forest	Albi-Boric Argosols
DL	115°25′24″	39°57′27″	972	6.6	539	Warm temperate deciduous broad-leaved forest	Alfisols
TY	112°04′39″	36°41′43″	1668	6.0	644	Warm temperate deciduous broad-leaved forest	Alfisols
SN	110°29′43″	31°19′15″	1510	8.5	1447	Subtropical deciduous evergreen mixed forest	Inceptisols
JL	114°26′28″	24°35′05″	562	18.2	1770	Subtropical evergreen broad-leaved forest	Ultisols
DH	112°32′14″	23°10′25″	240	21.8	1927	Subtropical monsoon evergreen broad-leaved forest	Ultisols
JF	108°51′26″	18°44′18″	809	23.2	2266	Tropical monsoon forest	Ultisols

751 a:HZ, Huzhong; LS, Liangshui; CB, Changbai; DL, Dongling; TY,Taiyue; SN, Shennong; JL, Jiulian; DH, Dinghu; JF, Jiangfeng.

752 b: MAT, mean annual temperature; MAP, mean annual precipitation.

753 **Table 2.** Soil properties of different sampling sites

Sampling site	pH	ST (°C)	SMC (%)	Silt (%)	SOC (g kg^{-1})	MBC (mg kg^{-1})	DOC (mg kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})
HZ	6.79±0.02a	10.3±0.15g	45.3±0.90c	56±1.2c	42.29±0.47b	350±6.0a	240±7.6e	2.90±0.16d	0.87±0.02b
LS	6.17±0.02b	15.9±0.02f	46.9±0.76c	64±0.3b	62.08±7.20a	316±0.7a	204±4.9f	4.59±0.29b	0.59±0.02c
CB	6.37±0.04b	16.0±0.06f	102.8±0.25a	76±0.6a	72.38±2.00a	178±8.8b	314±8.6c	6.05±0.17a	1.67±0.08a
DL	6.87±0.02a	17.8±0.14e	32.4±0.30e	6±2.4e	38.83±0.41c	43±0.8e	284±2.6d	3.17±0.04d	0.56±0.01c
TY	6.85±0.05a	16.0±0.12f	36.0±0.23d	49±1.4d	41.34±2.75c	115±4.0c	226±13.8f	2.43±0.15e	0.52±0.01c
SN	6.93±0.01a	18.4±0.12d	50.5±0.63b	74±0.3a	36.13±1.26c	72±13.1e	311±13.2c	3.76±0.05c	0.81±0.01b
JL	5.57±0.19b	25.3±0.01a	39.0±0.89d	68±0.3b	31.55±1.82c	89±19.7d	387±1.9b	2.28±0.09e	0.36±0.01d
DH	5.43±0.03c	24.4±0.04b	37.8±0.38d	50±1.8d	28.47±0.54d	38±0.1e	334±7.7c	1.77±0.02f	0.20±0.01e
JF	6.32±0.01c	22.5±0.07c	38.6±0.12d	49±0.2d	29.38±0.94d	140±1.3c	458±6.6a	1.99±0.02e	0.15±0.01e

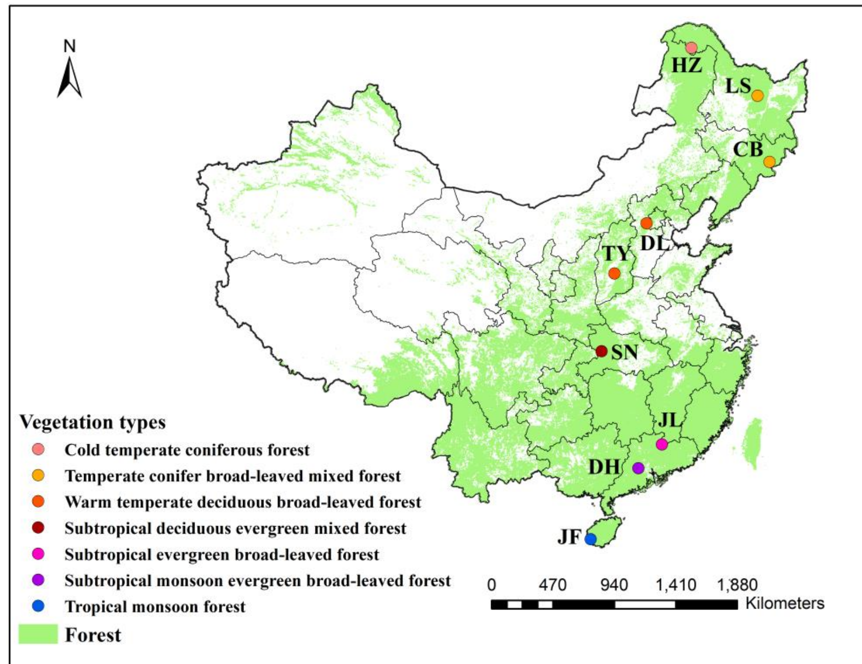
754 Note: ST=temperature of 0–10 cm soil; SMC=soil moisture content; Silt=soil silt content; SOC=soil organic carbon; MBC=microbial biomass carbon; DOC=dissolved organic carbon; TN=soil
755 total nitrogen; TP=soil total phosphorus. Values were presented as means ± SE (n=4). The abbreviations of the sampling sites were given in the Table 1.

756 **Table 3.** Functional diversity of soil microbial communities in forest ecosystems along the NSTEC

Sampling sites	Richness (*R*)	Shannon *H′*	Shannon *E*	Simpson *D*
HZ	14.08±0.34d	2.65±0.03d	1.01±0.007b	0.91±0.002c
LS	25.29±0.14b	3.12±0.02b	0.98±0.003c	0.95±0.001a
CB	27.00±0.27a	3.22±0.01a	0.98±0.001c	0.95±0.001a
DL	11.54±0.47e	2.52±0.03e	1.04±0.010a	0.87±0.005d
TY	22.33±0.87c	3.02±0.02c	0.98±0.002c	0.94±0.001a
SN	28.10±0.34a	3.24±0.01a	0.97±0.001c	0.95±0.001a
JL	23.54±0.07c	3.04±0.01c	0.96±0.001c	0.93±0.003b
DH	25.65±0.71b	3.11±0.01b	0.97±0.001c	0.93±0.002b
JF	27.63±0.68a	3.19±0.02a	0.96±0.001c	0.95±0.002a

757 Indices were calculated based on the optical density values after incubation for 96 h. Data are expressed as
758 means±standard errors. Different lowercase letters indicate significant differences among forests. The abbreviations
759 of the sampling sites are the same as those used in Table 1.

760 # Figures



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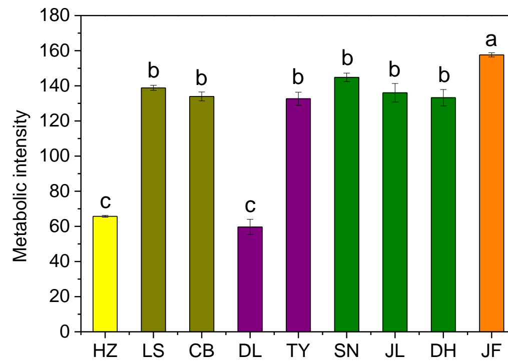

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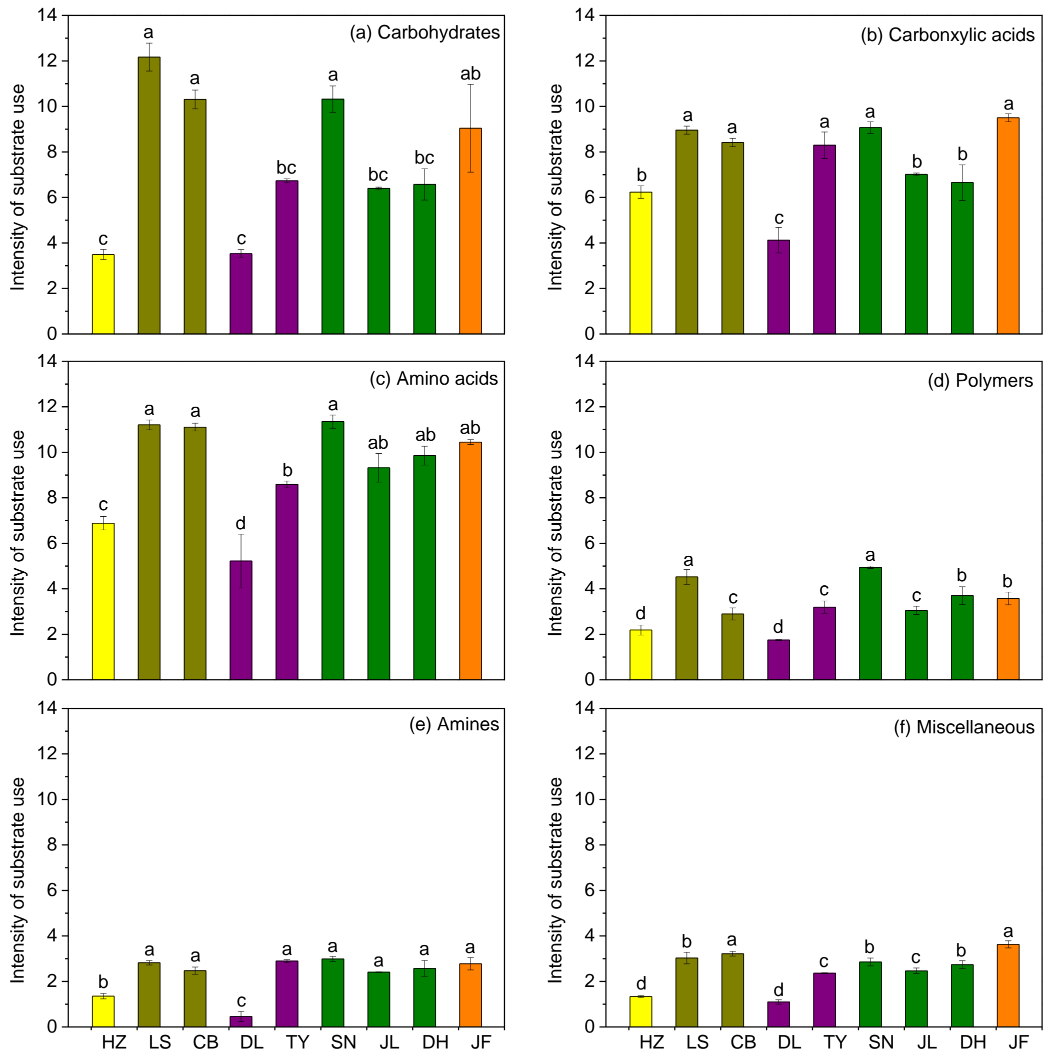

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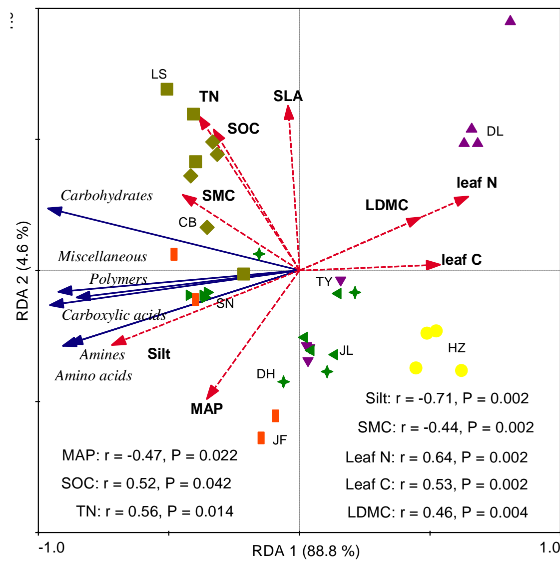

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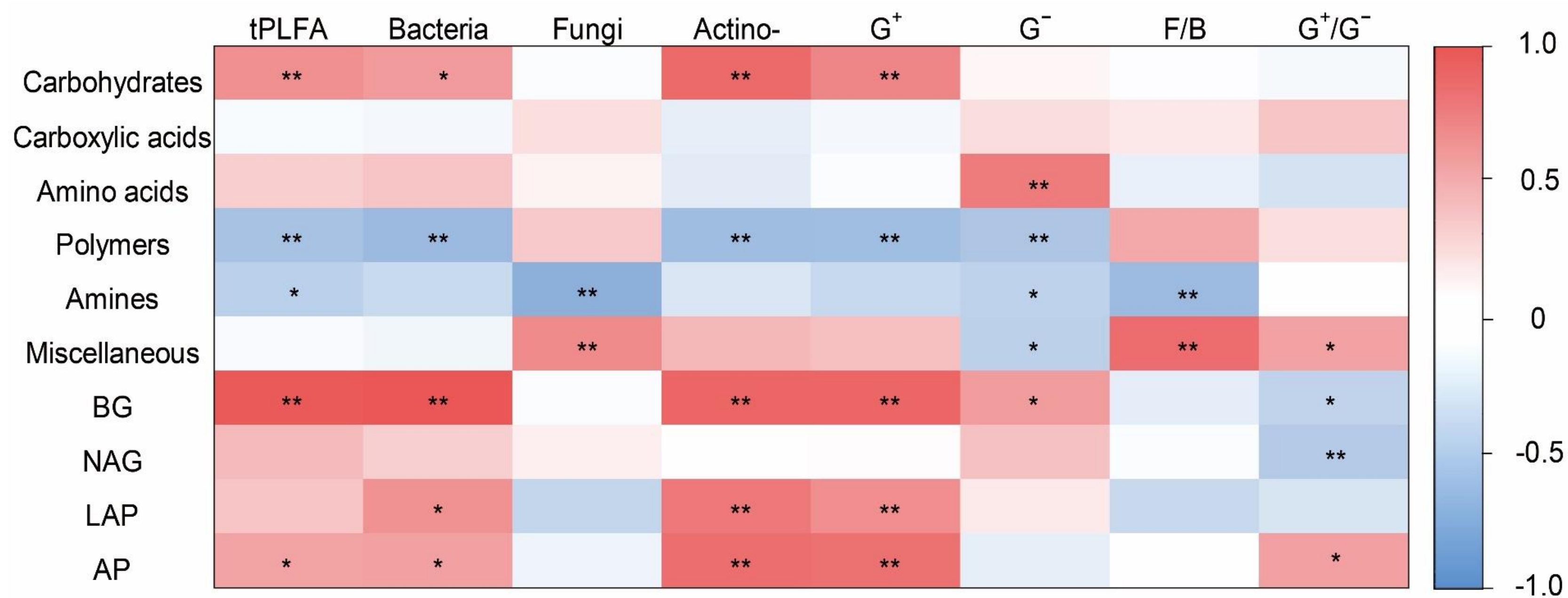

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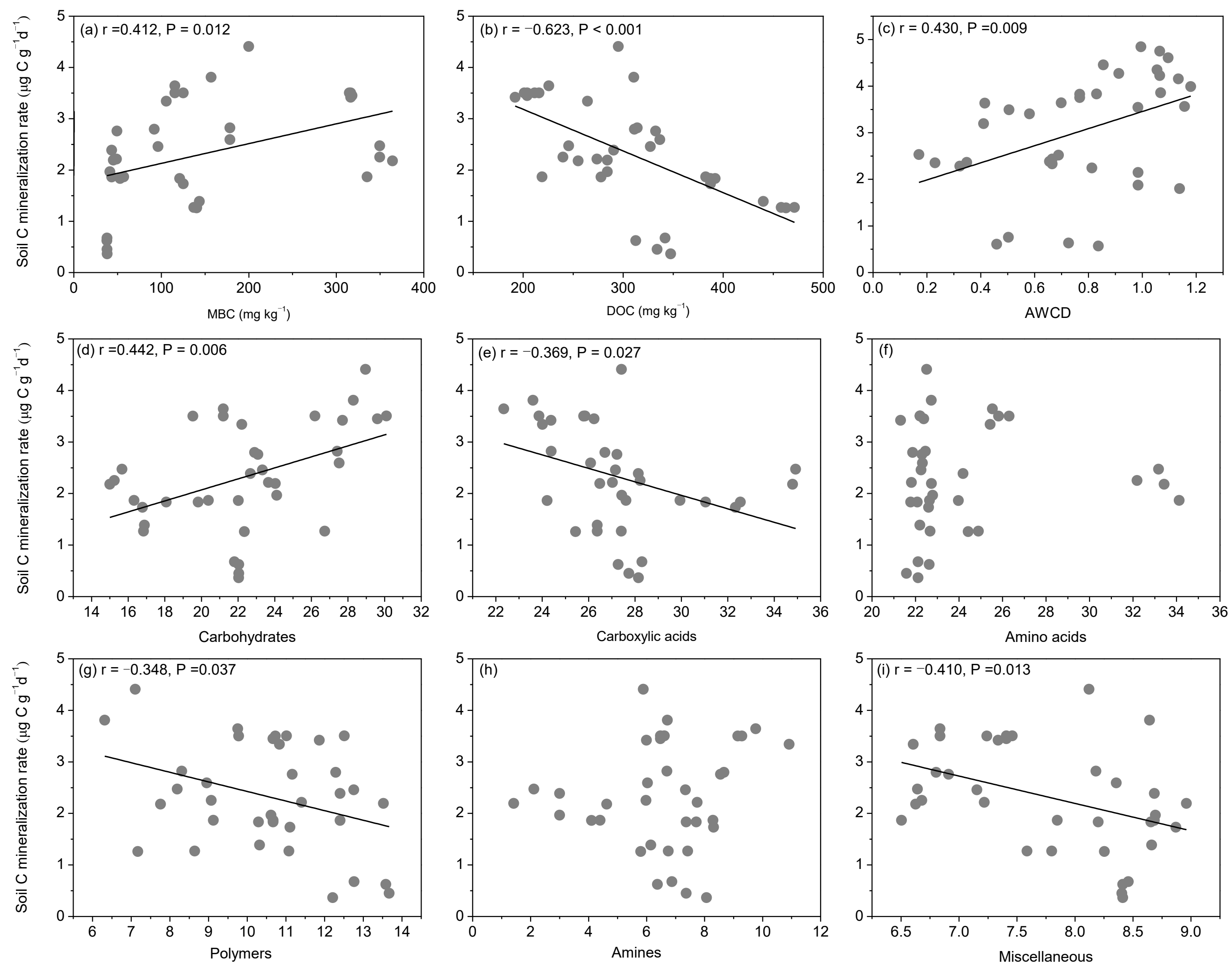

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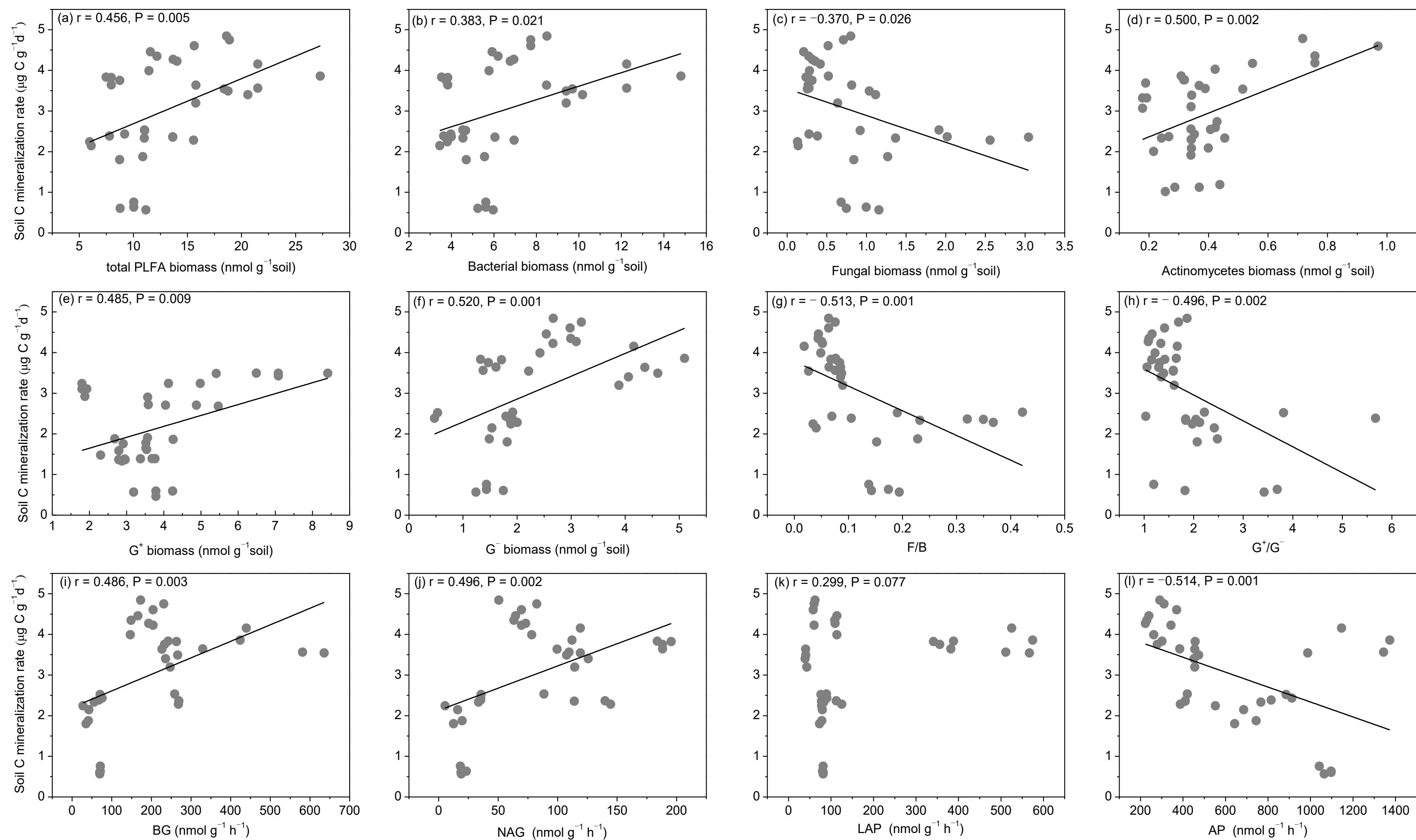

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