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Plant functional traits determined the latitudinal variations in soil microbial functions: evidence from a forest transect in China

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Abstract. Plant functional traits have increasingly been studied as determinants of ecosystem properties, especially for soil biogeochemical processes. While the relationships between biological community structures and ecological functions are a central issue in ecological theory, these relationships remain poorly understood at the large scale. We selected nine forests along the North–South Transect of Eastern China (NSTEC) to determine how plant functional traits influence the latitudinal pattern of soil microbial functions, and how soil microbial communities and functions are linked at the regional scale. We found that there was considerable variation in the profiles of different substrate use along the NSTEC. Soil microorganisms from temperate forests mainly metabolized high-energy substrates, while those from subtropical forests used all the substrates equally. The soil silt content and plant functional traits together shaped the biogeographical pattern of the soil microbial substrate use. Soil organic matter decomposition rates were significantly higher in temperate forests than in subtropical and tropical forests, which was consistent with the pattern of soil microbial biomass carbon concentrations. Soil organic matter decomposition rates were also significantly and negatively related to soil dissolved organic carbon concentrations, and carboxylic acid, polymer, and miscellaneous substrates. The soil microbial community structures and functions were significantly correlated along the NSTEC. Soil carbohydrate and polymer substrate use were mainly related to soil G^+ bacterial and actinomycetes biomass, while the use of amine and miscellaneous substrates were related to soil G^- bacteria, fungal biomass, and the F/B ratio. The contributions of different groups of microbial biomass to the production of soil enzyme activities differed. The relationship between soil microbial community structure and functions supported that there was functional dissimilarity.

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1 Introduction

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

Numerous studies have documented how environmental and anthropogenic perturbations impact on the structure, diversity (Zhou et al., 2016), and enzyme activities (Peng and Wang, 2016; Xu et al., 2017) of soil microbial communities (Tu et al., 2016), and have reported forests in the same climatic zone develop similar microbial communities. Other researchers have examined spatial patterns in soil microbial function at different scales. For example, in their study of Changbai Mountain, China, Tian et al. (2015) found that the soil microbial metabolic activity was moderately spatially dependent, and that the functional diversity was much more spatially dependent. Other researchers have reported differences in soil microbial activities among forest types, with high local variation and significant separation along regional climate gradients (Brockett et al., 2012; Cao et al., 2016). Soil microbes from different climatic zones have different affinities for carbon substrates. For example, microorganisms from boreal pine forest soils used carboxylic acids more efficiently, but decomposed amino acids much less efficiently, than microorganisms from temperate forest soils (Klimek et al., 2016). Despite this, because of limitations in analytical methods, questions still remain about how soil microbial functions vary at the regional scale.

The functional diversity of soil microbial communities is regulated by physico-chemical soil properties (Gartzia-Bengoetxea et al., 2016), climate (Cao et al., 2016), and the composition of plant cover (Sherman and Steinberger, 2012). For example, the geographic patterns of soil microbial activity reflect the climate, soil pH, and total phosphorus concentrations over large spatial scales (Cao

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

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

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decomposition of pine needles and soil organic matter, but G^- bacteria were mainly responsible for the decomposition of starch and xylose, which are easy to break down. Philippot et al. (2013), when studying the diversity of denitrifiers, showed that the loss of microbial diversity could result in decreases of between 4- and 5-fold in denitrification activity. In the Mediterranean, losses in the mass of decomposing leaf litter from shrub species accelerated as detritivore assemblages became more functionally dissimilar (Coulis et al., 2015). These studies suggest that the importance of functional redundancy in soil microbial communities has been overstated, so studies of the relationships between soil microbial communities and their functions in natural ecosystems are urgently needed.

The North-South Transect of Eastern China (NSTEC) extends from a cold temperate coniferous forest in the north to a tropical rainforest in the south, and includes almost all the forest types found in the Northern Hemisphere (Zhang and Yang, 1995) (Fig. 1 and Table 1). This transect, therefore, provides the optimal environment for investigating geographical patterns in microbial communities and their responses to environmental changes at the large scale. In this study, we examined spatial patterns in soil labile C concentrations, soil organic matter (SOM) decomposition rates, and metabolic activity and functional diversity of microbes in nine forest biomes along the NSTEC. We assessed how abiotic factors, such as climate, soil physical and chemical properties, and biotic factors, in the form of community-weighted means (CWM) of plant functional traits, contributed to soil functional diversity at the regional scale. We also examined the links between soil microbial community structure (PLFAs) and function (SOM decomposition rate, enzyme activities, and microbial substrate use). We tested the following three hypotheses in this study, that (1) the profiles of soil microbial substrate use would vary along a latitudinal gradient, (2) biogeographical patterns of soil microbial substrate use would be constrained by climate and plant functional traits, and (3) the relationships between soil microbial community and functions would demonstrate functional dissimilarity.

2 Material and methods

2.1 Study area and soil sampling

We selected nine forest ecosystems along the NSTEC, namely Huzhong (HZ), Liangshui (LS),

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131 Changbai (CB), Dongling (DL), Taiyue (TY), Shennong (SN), Jiulian (JL), Dinghu (DH), and
132 Jianfeng (JF) (18°44′–51°46′N, 128°53′–108°51′E) (Fig. 1, Table 1). For further information
133 regarding soil characterization and site descriptions see Xu et al. (2017). Forest soils have been
134 classified following the U.S. soil taxonomy and are described in Table 1 (Soil Survey Staff, 2010),
135 where information about the climate and the dominant vegetation at each site is also presented.

136 Soil samples were collected from four random plots in July and August 2013. The information
137 of the sampling process are available in Xu et al. (2017). Briefly, we established four sampling plots
138 measured 30 × 40 m and collected soil samples from a depth of between 0 and 10 cm at between 30
139 and 50 points in each plot along an S-shape. On return to the laboratory, the fresh soil samples were
140 immediately sieved through a 2-mm mesh and subdivided into three subsamples. One subsample was
141 stored briefly at 4°C until analysis for soil enzyme activities and soil pH. Another was stored briefly
142 at −20°C until analysis for PLFAs and Eco-Biolog. The third was air-dried, sieved through a 0.25
143 mm mesh, and analyzed for soil nutrients.

144 2.2 Soil analysis

145 Soil pH was measured at a soil-to-water ratio of 1:2.5. Soil organic carbon (SOC) and total N (TN)
146 concentrations were determined by dry combustion of ground samples (100-mesh) in a C/N analyzer
147 (Elementar, Vario Max CN, Germany). Total phosphorus (TP) was determined with a flow injection
148 auto-analyzer following digestion with H_2SO_4-$HClO_4$ (Huang et al., 2011). After extraction with
149 distilled water at a soil: distilled water ratio of 1:5, dissolved organic carbon (DOC) concentrations
150 were determined by Liqui TOC II (Elementar, Liqui TOC II, Germany) (Jones and Willett, 2006).
151 Soil microbial biomass carbon (MBC) was measured using the chloroform fumigation and direct
152 extraction technique (Vance et al., 1987). A conversion factor of 2.64 was used to convert extracted
153 C to biomass C. The silt fractions (<53 μm) of the samples were separated by wet-sieving and then
154 were freeze-dried in the laboratory, as described by Six et al. (2000). The soil properties are shown
155 in Table 2. We followed the method described by Bååth et al. (2003) for PLFA analysis and PLFAs
156 are expressed in units of nmol g^{-1}. The four enzymatic activities of β-glucosidase (BG), N-
157 acetylglucosaminidase (NAG), acid phosphatase (AP), and leucine aminopeptidase (LAP)
158 responsible for soil C, N, and phosphorous cycling, were measured following the procedure outlined

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in Saiya-Cork et al. (2002) and are expressed in units of nmol h^{-1} g^{-1}. Information about PLFA and enzyme activities are presented in Table S1.

2.3 Vegetation data

As described by Xu et al. (2018), we collected litter and sun-exposed and mature leaves (leaf blades for trees) from between five and ten individuals of each plant species at each site and determined their TN and TC concentrations. We calculated the specific leaf area (SLA, the one-sided area of a fresh leaf divided by its oven-dried mass, m^2 kg^{-1}), leaf dry matter content (LDMC, the oven-dried mass of a leaf divided by its water-saturated fresh mass, mg g^{-1}), leaf C concentrations (leaf C, g kg^{-1}), and leaf N concentrations (leaf N, g kg^{-1}) for ten fully expanded leaves of each sampled individual. We also calculated the community-weighted means (CWM), as described by Garnier et al. (2004). The diversity of the tree species and plant functional traits are summarized in Table S2.

2.4 Microbial substrate use

Microbial functional diversities were determined using a Biolog EcoPlate™ (Biolog Inc., Hayward, California, USA) as described by Garland and Mills (1991). Briefly, approximately 10 g of fresh soil was suspended in 100 ml saline solution (0.85% NaCl) and shaken on an orbital shaker for 30 min at 190 rpm. A 150 µl aliquot of supernatant from 1:1 000 dilutions of each soil sample was added to each well. The plates were incubated at 25°C, and the absorbance at 590 nm was measured using a microplate reader (GENios Pro™, Tecan Trading AG, Männedorf, Switzerland) every 24 h up to 240 h (0, 24, 48, 72, 96, 20, 144, 168, 192, 216, and 240 h).

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

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

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

2.5 SOM decomposition rate

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

2.6 Statistical analysis

One-way analysis of variance (ANOVA) followed by a post hoc Tukey HSD test were used to test the significance of the differences among the soil properties, C use, functional diversity, and SOM decomposition rates in the different forest ecosystems. We tested the relationships between labile C, soil microbial community structure, microbial function, and the SOM decomposition rates with the Pearson correlation test. Differences were considered significant when $P<0.05$, with marginal significance set at $P<0.01$. All ANOVA and regression analyses were performed using SPSS 19.0 for Windows. Data are reported as the mean ± SE.

We used redundancy analysis (RDA) to examine the relationship between the environmental variables and soil microbial substrate use. The environmental variables were the same as those described in Xu et al. (2018), including climate, soil properties, litter properties, and plant functional traits. Before RDA, we conducted forward selection of the environmental variables that were significantly correlated with variations in the microbial substrate use profile using stepwise regression and the Monte Carlo Permutation Test. We used CANOCO software 4.5 (Ter Braak and Smilauer 2002) for the RDA and stepwise regression. The environmental properties, which were significantly correlated with the microbial substrate use in the RDA, were stressed in the plots.

3 Results

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212 3.1 Patterns in the microbial substrate use, soil labile carbon, and SOM decomposition rates

213 Of the forests along the NSTEC, the C metabolic intensity of soil microbes was lowest in HZ and LS;
214 the C metabolic intensity of soil microbes differed significantly between JF and the other forests (Fig.
215 2), which indicates that the color development was significantly higher in the tropical forest soils
216 than in the subtropical and temperate forest soils and is consistent with the variations in the AWCD
217 (Fig.S1). The average values of *R*, *H'*, and *D* were significantly different among the nine forest soils
218 and were highest in JF, SN, and CB (Table 3).

219 Across the nine forests, soil microorganisms used the six substrate groups in the same order; the
220 carboxylic acid substrate was used most, followed by amino acids, carbohydrates, polymers, amines,
221 and miscellaneous substrates (Fig. 3). Microorganisms in the boreal and temperate forests mainly
222 metabolized carbohydrates, amino acids, and carboxylic acids, while those from the subtropical and
223 tropical forests used the substrates in equal proportions.

224 Overall, soil MBC concentrations in the boreal and temperate forests were three to eight times
225 higher than those of the subtropical and tropical forests. In contrast, the average DOC concentration
226 in the tropical and subtropical forest soils ranged from 311 to 458 mg kg^{-1}, which was significantly
227 higher than the average concentration in the temperate and boreal forest soils, where the average
228 concentrations ranged from 204 to 284 mg kg^{-1} (Table 2). The average SOM decomposition rates in
229 the subtropical forests ranged from 0.64 to 2.42 μg C g^{-1} d^{-1}, and were significantly lower than the
230 rates in the temperate forests, which ranged from 3.43 to 4.61 μg C g^{-1} d^{-1} (Table S3).

231 3.2 Effect of environmental properties on soil microbial substrate use

232 Redundancy analysis showed that the variations in soil microbial substrate use were strongly and
233 positively correlated with the CWM values of LDMC, leaf N, and leaf C, and strongly and negatively
234 correlated with the soil silt content and SMC (Fig. 4). The RDA2 of soil microbial substrate use was
235 strongly positively correlated with TN and SOC, but negatively correlated with mean annual
236 precipitation (MAP) (Fig. 5). RDA1 mainly represented the plant functional traits, soil texture, and
237 micro-meteorological conditions, while RDA2 represented climate and soil nutrients. Overall, the
238 soil silt content and the CWM values of plant functional traits were the main predictors of the

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latitudinal variation in the soil microbial substrate use along the NSTEC.

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

Microbial carbohydrate use was positively related with bacterial biomass and actinomycic biomass (Fig.5). Microbial polymer use was negatively related with bacterial biomass and actinomycic biomass. Microbial amines use was negatively related with G^- bacterial and fungal biomass. Miscellaneous substrate use was positively related with fungal biomass and G^+/G^- bacterial biomass (Fig.5).

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

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

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

The SOM decomposition rates were significantly and positively correlated with total PLFAs (r=0.456, P=0.005), bacteria (r=0.3836, P=0.021), actinomycetes (r=0.500, P=0.002), and G^- bacteria PLFAs (r=0.520, P=0.001) (Fig. 7a, b, d, and f) but were negatively correlated with fungal 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, g, and h). Except for LAP activity, soil enzyme activities were significantly and positively correlated with the SOM decomposition rates (P<0.01) (Fig. 7i, j, and l).

4 Discussion

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

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

Heterotrophic soil respiration is sustained by the decomposition of SOM. The SOM decomposition rates along the NSTEC were greater in temperate forests than in subtropical forests, which was consistent with the variations in the soil MBC and SOC concentrations. These results indicate that, as found in other studies, large scale SOM decomposition rates are driven by the amounts of substrate available (Yu et al., 2010). Changes in the availability of C in SOM may affect the microbial resource strategies, which may in turn influence the SOM decomposition rate.

4.2 Latitudinal variation in microbial substrate use

The AWCD reflects the sole C source use ability of the soil microbial community (Garland and Mills, 1991). Of the six groups of C substrates, microbial communities in the temperate forests mainly used carbohydrates, carboxylic acids, and amino acids, which suggests that microorganisms in temperate forests probably use high-energy substrates that degrade easily (Kunito et al., 2009). The latitudinal pattern of soil microbial C substrate use was mainly related to the soil silt contents and the CWMs of LDMC, leaf C, and leaf N concentrations, indicating that the quality of nutrients from plant inputs had a major influence on microbial carbon use efficiency. Plant species with high SLA, high N

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292 concentrations in leaves, and low LDMC can result in bacterial-dominated soil microbial
293 communities in grasslands (Orwin et al., 2010). Looking beyond individual traits, related tree species
294 may cultivate microbial communities with similar preference for carbon sources through the
295 coevolution of plants and microbes (Liu et al., 2012; Buscot, 2015).

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

307 We also found that the C substrate use was negatively correlated with the leaf C concentrations
308 (Table S2). High latitude plants may have higher leaf C concentrations than plants at lower latitudes
309 so that they can balance the osmotic pressure of cells and resist freezing (Millard et al., 2007; Hoch
310 and Körner, 2012). The increased C was most likely in the form of an increase in non-structural C,
311 including starch, low molecular weight sugars, and storage lipids that are easy to break down. Plant
312 functional traits play an important role in shaping soil microbial communities (Pei et al., 2016), so
313 soil microorganisms from the temperate forests mainly metabolized high-energy substrates
314 (carbohydrates, carboxylic acids, and amino acids).

315 The LDMC is the ratio of the leaf dry weight to the fresh weight and has been used as a proxy
316 for the ratio of structural compounds to assimilatory tissue (mesophyll and epidermis, Van Arendonk
317 and Poorter, 1994). High values of LDMC indicate large amounts of vascular tissue, cellulose,
318 insoluble sugars, and leaf lignin that are difficult to decompose (Poorter and Bergkotte, 1992); C
319 substrates such as carbohydrates, carboxylic acid, and amino acid are, however, easy to decompose
320 (Myers et al., 2001). In line with this, the use of carbohydrate, carboxylic acid, and amino acid

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substrates was negatively related to the CWMs of the LDMC (Table S2). Pei et al. (2016) reported that the LDMC was an important driver of multivariate soil microbial community structure and G^- bacterial abundance.

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

4.3 Links between soil microbial community structure and function

The quality and changes in the amounts of SOM are influenced by the biomass, vegetation coverage, root distribution, microbial specie (Raich and Schlesinger, 1992). The SOM decomposition rates were higher in temperate forests than in tropical forests and may reflect the higher soil microbial biomass (Wang et al., 2016). In line with this, SOM decomposition rates were positively related with soil MBC concentrations and different groups of PLFAs. The inverse relationships between SOM decomposition rates and DOC, and between SOM decomposition rates and the use of some individual C substrates along the NSTEC, indicate a shift in the soil C turnover from open to closed with increases in the soil labile C concentrations. Further, soil nutrients have a strong influence on the spatial patterns of soil microbial communities. Thus, soil DOC and MBC do not influence SOM decomposition rates directly, but indirectly by regulating microbial properties (Boberg et al., 2014; Wei et al., 2014). Because different communities of microbes have different SOM use efficiencies (Balser and Wixon, 2009; Lipson et al., 2009; Monson et al., 2006), changes in the microbial community structure may influence the decomposition rates of organic matter (Lipson et al., 2009; Keiblinger et al., 2010).

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Shifts in microbial community composition may influence enzyme production (DeForest et al., 2012; Waldrop et al., 2000; Brockett et al., 2012). Different microbial groups require different amounts of nutrients to construct biomass, or have enzymes that differ in their affinity for nutrients. For example, fungi tend to have higher C/N or C/P ratios while heterotrophic bacteria typically have lower C/N or C/P ratios (Sterner and Elser, 2002). We found that the relative abundances of the G^+ bacteria and actinomycetes communities were associated with the specific activities of hydrolytic enzymes involved in C and N acquisition (BG and LAP), whereas the relative abundance of the G^- bacteria was correlated with soil NAG activities involved in chitin degradation. Waldrop et al. (2000) found that phosphatase activity was significantly correlated with the abundance of various bacterial PLFAs. Soil BG was mainly responsible for cellulose degradation and was involved in breaking down complex organic compounds (cellobiose) into small molecule substrates (glucose) in favor of acquiring C through microbial community growth. Other studies have found that G^+ bacteria were positively correlated with the cellobiohydrolase that was responsible for degrading complex compounds (Waldrop et al., 2000). Fungi are commonly considered as producers of oxidative enzymes. Therefore, the influence of fungal biomass on variations in enzyme activities was minimal (Kivlin and Treseder, 2014). The linkages between enzyme activity and community composition may provide some insight into the microbial mechanisms that drive the decomposition of macromolecular C compounds.

The soil microbial community structure and functions were significantly correlated along the NSTEC. Soil carbohydrate and polymer substrate use were mainly related to soil G^+ bacterial and actinomycic biomass, but amines and miscellaneous substrates were mainly related to soil G^- bacterial, fungal biomass, and the F/B ratio. Soil bacteria mainly decomposed simple carbohydrates, organic acids, and amino acids, whereas soil fungi mainly decomposed recalcitrant compounds (Myers et al., 2001; Treonis et al., 2004). Shifts in the microbial community composition may influence enzyme production if microbial groups need nutrients at lower concentrations to construct biomass, or have enzymes that differ in their affinity for nutrients. In agreement with our study, numerous other researchers have reported significant correlations between PLFA profiles and enzyme activities (DeForest et al., 2012; Brockett et al., 2012; Riah-Anglet et al., 2015). Soil BG and AP activities were positively related with bacterial and actinomycic biomass and negatively related with

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fungal biomass. Soil NAG activities were weakly and positively related with fungal biomass in the present study, and may have been mainly produced by fungal populations (Valášková et al., 2007). These results suggest that that overall ecosystem functioning may suffer if soil microbial groups are lost, which confirms the functional dissimilarity hypothesis. However, to gain an improved understanding of the mechanisms that drive these relationships, we need to carry out further studies with different experimental techniques.

5 Conclusions

In this study we examined the patterns in labile C concentrations, SOM decomposition rates, microbial substrate use, and functional diversity and identified a combination of abiotic and biotic factors that influenced soil microbial functional diversity at the regional scale. The MBC concentration and SOM decomposition rates were significantly lower, and the soil DOC concentrations and microbial metabolic activities were higher, in the subtropical and tropical forests than in the temperate forests. For the first time, we showed that, along with the soil silt content, CWM plant traits explained variations in soil microbial C substrate use at the regional scale. Soil microbial community structure and function were strongly related, which suggest that the loss of soil microbial groups may have consequences for overall ecosystem functioning, which confirms the functional dissimilarity hypothesis.

Data accessibility. Requests for data and materials should be addressed to N.H. (henp@igsnrr.ac.cn) and G.Y. (yugr@igsnrr.ac.cn).

Author contributions. Z.W.X., G.R.Y. and X.Y.Z. planned and designed the research. Z.W.X., N.P.H., R.L.W., and N.Z. conducted fieldwork. Z.W.X., G.R.Y., X.Y.Z., and Q.F.W wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests. The authors declare that they have no conflict of interest.

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References

van Arendonk, J.J.C.M., Poorter, H. The chemical composition and anatomical structure of leaves of grass species differing in relative growth rate, Plant Cell Environ., 17, 963-970, 1994.

Bååth, E., Anderson, T.H. Comparison of soil fungal/bacterial ratios in a pH gradient using physiological and PLFA-based techniques, Soil Biol. Biochem., 35, 955-963, 2003.

Balser, T.C., Firestone, M.K. Linking microbial community composition and soil processes in a California annual grassland and mixed-conifer forest,Biogeochemistry, 73, 395-415, 2005.

Balser, T.C., Wixon, D.L. Investigating biological control over soil carbon temperature sensitivity, Global Change Biol., 15, 2935-2949, 2009.

Banerjee, S., Kirkby, C.A., Schmutter, D., Bissett, A., Kirkegaard, J.A., Richardson, A.E. Network analysis reveals functional redundancy and keystone taxa amongst bacterial and fungal communities during organic matter decomposition in an arable soil, Soil Biol. Biochem., 97, 188-198, 2016.

Boberg, J.B., Finlay, R.D., Stenlid, J., Ekblad, A., Lindahl, B.D. Nitrogen and carbon reallocation in fungal mycelia during decomposition of boreal forest litter, PLOS ONE, 9, e92897, 2014.

Brockett, B.F.T., Prescott, C.E., Grayston, S.J.. Soil moisture is the major factor influencing microbial community structure and enzyme activities across seven biogeoclimatic zones in western Canada, Soil Biol. Biochem., 44, 9-20, 2012.

Buscot, F. Implication of evolution and diversity in arbuscular and ectomycorrhizal symbioses, J. Plant Physiol., 172, 55-61, 2015.

Cao, H., Chen, R., Wang, L., Jiang, L., Yang, F., Zheng, S., Wang, G., Lin, X. Soil pH, total phosphorus, climate and distance are the major factors influencing microbial activity at a regional spatial scale, Sci. Rep-UK, 6, 25815, 2016.

Carson, J.K., Gonzalez-Quinones, V., Murphy, D.V., Hinz, C., Shaw, J.A., Gleeson, D.B. Low pore connectivity increases bacterial diversity in soil, Appl. Environ. Microb., 76, 3936-3942, 2010.

Coulis, M., Fromin, N., David, J.-F., Gavinet, J., Clet, A., Devidal, S., Roy, J., Hättenschwiler, S. Functional dissimilarity across trophic levels as a driver of soil processes in a Mediterranean decomposer system exposed to two moisture levels, Oikos, 124, 1304-1316, 2015..

De Vries, F.T., Manning, P., Tallowin, J.R., Mortimer, S.R., Pilgrim, E.S., Harrison, K.A., Hobbs, P.J., Quirk, H., Shipley, B., Cornelissen, J.H., Kattge, J., Bardgett, R.D. Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities, Ecol. Lett., 15, 1230-1239, 2012.

Deforest, J., Smemo, K., Burke, D., Elliott, H., Becker, J. Soil microbial responses to elevated phosphorus and pH in acidic temperate deciduous forests, Biogeochemistry, 109, 189-202, 2012.

Fang, H., Cheng, S., Wang, Y., Yu, G., Xu, M., Dang, X., Li, L., Wang, L. Changes in soil heterotrophic respiration, carbon availability, and microbial function in seven forests along a climate gradient, Ecol. Res., 29, 1077-1086, 2014.

Fiere, N., Bradford, M. A. Toward an ecological classification of soil bacteria, Ecology, 88,1354-1364, 2007.

Garland, J.L., Mills, A.L. Classification and characterization of heterotrophic microbial communities on the basis of patterns of community-level sole carbon source utilization, Appl. Environ. Microb., 57, 2351-2359, 1991.

Garnier, E., Cortez, J., Billes, G., Navas, M.L., Roumet, C., Debussche, M., Gérard, L., Alain, B., David, A., Astrid, B., Cathy, N., Jean-Patrick, T. Plant functional markers capture ecosystem properties during secondary succession, Ecology, 85, 2630-2637, 2004.

Gartzia-Bengoetxea, N., Kandeler, E., Martínez de Arano, I., Arias-González, A. Soil microbial functional activity is governed by a combination of tree species composition and soil properties in temperate forests, Appl. Soil Ecol., 100, 57-64, 2016.

Gomez, E., Ferreras, L., Toresani, S. Soil bacterial functional diversity as influenced by organic amendment application, Bioresour. Technol., 97, 1484-1489, 2006.

Guckert, J.B., Carr, G.J., Johnson, T.D., et al. Community analysis by Biolog: curve integration for statistical analysis of activated sludge microbial habitats, J. Microbiol. Meth., 27, 183-197, 1996.

Huang, Z., Clinton, P.W., Baisden, W.T., Davis, M.R. Long-term nitrogen additions increased surface soil carbon concentration in a forest plantation despite elevated decomposition, Soil Biol. Biochem., 43, 302-307, 2011.

Jagadamma, S., Mayes, M.A., Steinweg, J.M., Schaeffer, S.M. Substrate quality alters the microbial mineralization of added substrate and soil organic carbon, Biogeosciences, 11, 4665-4678, 2014.

Jones, D., Willett, V. Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil, Soil Biol. Biochem., 38, 991-999, 2006.

Keiblinger, K.M., Hall, E.K., Wanek, W., Szukics, U., Hammerle, I., Ellersdorfer, G., Bock, S., Strauss, J., Sterflinger, K., Richter, A., Zechmeister-Boltenstern, S. The effect of resource quantity and resource stoichiometry on microbial carbon-use-efficiency. FEMS Microb. Ecol. 73, 430-440, 2010.

Kivlin, S.N. & Treseder, K.K. Soil extracellular enzyme activities correspond with abiotic factors more than fungal community composition, Biogeochemistry, 117, 23-37, 2014.

Klimek, B., Chodak, M., Jaźwa, M., Niklińska, M. Functional diversity of soil microbial communities in boreal and temperate Scots pine forests, Eur. J. Forest Res., 135, 731-742, 2016.

Kunito, T., Akagi, Y., Park, H.-D., Toda, H. Influences of nitrogen and phosphorus addition on polyphenol oxidase activity in a forested Andisol, Eur. J. Forest Res., 128, 361-366, 2009.

Lipson, D.A., Monson, R.K., Schmidt, S.K., Weintraub, M.N. The trade-off between growth rate and yield in microbial communities and the consequences for under-snow soil respiration in a high elevation coniferous forest, Biogeochemistry, 95, 23-35, 2009.

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Liu, X., Liang, M., Etienne, R.S., Wang, Y., Staehelin, C., Yu, S. Experimental evidence for a phylogenetic Janzen-Connell effect in a subtropical forest, Ecol. Lett., 15, 111-118, 2012.

Liu, Z., Liu, G., Fu, B., Wu, Y., Hu, H., Fu, S. Changes in the soil microbial community with a pine plantation restoration in a dry valley of the upper reaches of the Minjiang River, southwest China, Ann N Y Acad. Sci., 1195 Suppl 1, E82-95, 2010.

Millard, P., Sommerkorn, M., Grelet, G.A. Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal, New Phytol., 175, 11-28, 2007.

Monson, R.K., Lipson, D.L., Burns, S.P., Turnipseed, A.A., Delany, A.C., Williams, M.W., Schmidt, S.K. Winter forest soil respiration controlled by climate and microbial community composition,Nature, 439, 711-714, 2006.

Myers, R.T., Zak, D.R., White, D.C., Peacock, A. Landscape-level patterns of microbial community composition and substrate use in upland forest ecosystems, Soil Sci. Soc. Am. J., 65, 359-367, 2001.

Orwin, K.H., Buckland, S.M., Johnson, D., Turner, B.L., Smart, S., Oakley, S., Bardgett, R.D. Linkages of plant traits to soil properties and the functioning of temperate grassland, J. Ecol., 98, 1074-1083, 2010.

Pei, Z., Eichenberg, D., Bruelheide, H., Kröber, W., Kühn, P., Li, Y., von Oheimb, G., Purschke, O., Scholten, T., Buscot, F., Gutknecht, J.L.M. Soil and tree species traits both shape soil microbial communities during early growth of Chinese subtropical forests, Soil Biol. Biochem., 96, 180-190, 2016.

Peng, X., Wang, W. Stoichiometry of soil extracellular enzyme activity along a climatic transect in temperate grasslands of northern China, Soil Biol. Biochem., 98, 74-84, 2016.

Philippot, L., Spor, A., Henault, C., Bru, D., Bizouard, F., Jones, C.M., Sarr, A., Maron, P.A. Loss in microbial diversity affects nitrogen cycling in soil, ISME J., 7, 1609-1619, 2013.

Poorter, H., Bergkotte, M. Chemical composition of 24 wild species differing in relative growth rate, Plant Cell Environ.,15, 221-229, 1992.

Preston-Mafham, J., Boddy, L., Randerson, P.F. Analysis of microbial community functional diversity using sole-carbon-source utilisation profies-a critique, FEMS Microb. Ecol., 42, 1-14, 2002.

Raich, J.W., Clark, D.A., Schwendenmann, L., Wood, T.E. Aboveground tree growth varies with belowground carbon allocation in a tropical rainforest environment, PloS one, 9, e100275, 2014.

Riah-Anglet, W., Trinsoutrot-Gattin, I., Martin-Laurent, F., Laroche-Ajzenberg, E., Norini, M.-P., Latour, X., Laval, K. Soil microbial community structure and function relationships: A heat stress experiment, Appl. Soil Ecol., 86, 121-130, 2015..

Russell, A.E., Raich, J.W., Valverde-Barrantes, O.J., Fisher, R.F. Tree species effects on soil properties in experimental plantations in tropical moist forest, Soil Sci. Soc. Am. J., 71, 1389, 2007.

Saiya-Cork, K.R., Sinsabaugh, R.L., Zakb, D.R. The effects of long term nitrogen deposition on extracellular enzyme activity in an Acer saccharum forest soil, Soil Biol. Biochem., 34, 1309-1315, 2002.

Sessitsch, A., Weilharter, A., Gerzabek, M.H., Kirchmann, H., Kandeler, E. Microbial Population Structures in Soil Particle Size Fractions of a Long-Term Fertilizer Field Experiment, Appl. Environ. Microb., 67, 4215-4224, 2001.

Sherman, C., Steinberger, Y. Microbial functional diversity associated with plant litter decomposition along a climatic gradient, Microb. Ecol., 64, 399-415, 2012.

Six, J., Elliott, E. T., Paustian, K. Soil structure and soil organic matter: II. A normalized stability index and the effect of mineralogy, Soil Sci. Soc. Am. J., 64, 1042-1049, 2000.

Sterner, R. W. & Elser, J. J. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton, New Jersey, USA: Princeton University Press, 2002.

Strickland, M.S., Lauber, C., Fierer, N., Bradford, M.A. Testing the functional significance of microbial community composition, Ecology, 90, 441-451, 2009.

Soil Survey StaffKeys to Soil Taxonomy, 11th ed. USDA-Natural Resources Conservation Service, Washington, DC, 2010.

Swallow, M.J.B., Quideau, S.A. A method for determining community level physiological profiles of organic soil horizons, Soil Sci. Soc. Am. J., 79, 536-542, 2015.

Talbot, J.M., Bruns, T.D., Taylor, J.W., Smith, D.P., Branco, S., Glassman, S.I., Erlandson, S., Vilgalys, R., Liao, H.L., Smith, M.E., Peay, K.G. Endemism and functional convergence across the North American soil mycobiome, P. Natl. Acad. Sci. USA., 111, 6341-6346, 2014.

Ter Braak, C.J.F., Smilauer, P. CANOCO Reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (Version 4.5). Microcomputer, 2002.

Tian, H., Chen, G., Zhang, C., Melillo, J.M., Hall, C.A.S., Pattern and variation of C:N:P ratios in China's soils: a synthesis of observational data, Biogeochemistry, 98, 139-151 2010.

Tian, J., McCormack, L., Wang, J., Guo, D., Wang, Q., Zhang, X., Yu, G., Blagodatskaya, E., Kuzyakov, Y. Linkages between the soil organic matter fractions and the microbial metabolic functional diversity within a broad-leaved Korean pine forest, Eur. J. Soil Biol., 66, 57-64, 2015.

Treonis, A.M., Ostle, N.J., Stott, A.W., Primrose, R., Grayston, S.J., Ineson, P. Identification of groups of metabolically-active rhizosphere microorganisms by stable isotope probing of PLFAs, Soil Biol. Biochem., 36, 533-537, 2004.

Tu, Q., Deng, Y., Yan, Q., Shen, L., Lin, L., He, Z., Wu, L., Van Nostrand, J.D., Buzzard, V., Michaletz, S.T., Enquist, B.J., Weiser, M.D., Kaspari, M., Waide, R.B., Brown, J.H., Zhou, J. Biogeographic patterns of soil diazotrophic communities across six forests in the North America, Mol. Ecol., 25, 2937-2948, 2016.

Valášková, V., Šnajdr, J., Bittner, B., Cajthaml, T., Merhautová, V., Hofrichter, M., Baldrian, P. Production of lignocellulose-degrading enzymes and degradation of leaf litter by saprotrophic basidiomycetes isolated from a Quercus petraea forest, Soil Biol. Biochem., 39, 2651-2660, 2007.

Vance, E.D., Brookes, P.C., Jenkinson, D.S. An extraction method for measuring soil microbial biomass C, Soil Biol.

© Author(s) 2019. CC BY 4.0 License.

Biochem., 19, 703-707, 1987.
Veen, J.A.V., Kuikman, P.J. Soil structural aspects of decomposition of organic-matter by micro-organism, Biogeochemistry, 11, 213-233, 1990.
Waldrop, M.P., Firestone, M.K. Response of microbial community composition and function to soil climate change, Microb. Ecol., 52, 716-724, 2006.
Waldrop, M. P., Balser, T. C. & Firestone, M. K. Linking microbial community composition to function in a tropical soil,Soil Biol. Biochem., 32, 1837-1846, 2000.
Wang, Q., He, N., Yu, G., Gao, Y., Wen, X., Wang, R., Koerner, S.E., Yu, Q. Soil microbial respiration rate and temperature sensitivity along a north-south forest transect in eastern China: Patterns and influencing factors, J. Geophys. Res.(Biogeosciences), 121, 399-410, 2016.
Waring, B.G., Alvarez-Cansino, L., Barry, K.E., Becklund, K.K., Dale, S., Gei, M.G., Keller, A.B., Lopez, O.R., Markesteijn, L., Mangan, S., Riggs, C.E., Rodriguez-Ronderos, M.E., Segnitz, R.M., Schnitzer, S.A., Powers, J.S. Pervasive and strong effects of plants on soil chemistry: a meta-analysis of individual plant 'Zinke' effects, Proc. R. Soc. B. The Royal Society, 282, 20151001, 2015.
Wei, H., Guenet, B., Vicca, S., Nunan, N., AbdElgawad, H., Pouteau, V., Shen, W., Janssens, I.A. Thermal acclimation of organic matter decomposition in an artificial forest soil is related to shifts in microbial community structure, Soil Biol. Biochem., 71, 1-12, 2014.
Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., et al. The worldwide leaf economics spectrum, Nature, 428, 821-827, 2004.
Xu, X., Thornton, P.E., Post, W.M. A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems, Global Ecol. Biogeogr., 22, 737-749, 2013.
Xu, Z., Yu, G., Zhang, X., Ge, J., He, N., Wang, Q., Wang, D. The variations in soil microbial communities, enzyme activities and their relationships with soil organic matter decomposition along the northern slope of Changbai Mountain, Appl. Soil Ecol., 86, 19-29, 2015.
Xu, Z., Yu, G., Zhang, X., He, N., Wang, Q., Wang, S., Wang, R., Zhao, N., Jia, Y., Wang, C. Soil enzyme activity and stoichiometry in forest ecosystems along the North-South Transect in eastern China (NSTEC), Soil Biol. Biochem., 104, 152-163, , 2017.
Xu, Z., Yu, G., Zhang, X., He, N., Wang, Q., Wang, S., Xu, X., Wang, R., Zhao, N. Biogeographical patterns of soil microbial community as influenced by soil characteristics and climate across Chinese forest biomes, Appl. Soil Ecol., 124, 298-305, 2018.
Yu, G., Zheng, Z., Wang, Q., Fu, Y., Zhuang, J., Sun, X., Wang, Y. Spatiotemporal pattern of soil respiration of terrestrial ecosystems in China: the development of a geostatistical model and its simulation.,Environ. Sci. Technol., 44, 6074-6080, 2010.
Zak, J.C., Willig, M.R., Moorhead, D.L., Wildman, H.G. Functional diversity of microbial communities: a quantitative approach, Soil Biol. Biochem., 26, 1101-1108, 1994.
Zhang, X. S., Yang, D. A. Allocation and study on global change transects in China, Quaternary Sci., 1, 43-52, 1995. (In Chinese)
Zhou, J., Deng, Y., Shen, L., Wen, C., Yan, Q., Ning, D., Qin, Y., Xue, K., Wu, L., He, Z., Voordeckers, J.W., Nostrand, J.D., Buzzard, V., Michaletz, S.T., Enquist, B.J., Weiser, M.D., Kaspari, M., Waide, R., Yang, Y., Brown, J.H. Temperature mediates continental-scale diversity of microbes in forest soils, Nat. Commun., 7, 12083, 2016.

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Figures legends

Fig. 1. Distribution of typical forest ecosystems along the North-South Transect of eastern China (NSTEC). The abbreviations for the sampling sites from north to south are as follows: HZ, Huzhong; LS, Liangshui; CB, Changbai; DL, Dongling; TY, Taiyue; SN, Shennong; JL, Jiulian; DH, Dinghu; JF, Jiangfeng. These abbreviations are used for the nine forests throughout.

Fig.2. Variations in soil microbial substrate use during a 240-h incubation for the nine forests. Different colors represent different forest types: Yellow, coniferous forest; Dark yellow, coniferous broad-leaved mixed forest; Purple, deciduous broad-leaved forest; Olive, subtropical evergreen broad-leaved forest; Orange, Tropical monsoon forest. Different lowercase letters indicate significant differences among forests in the same climate zone. The abbreviations of the sampling sites are given in Table 1.

Fig. 3. Characteristics of microbial use of (a) carbohydrates, (b) carboxylic acids, (c) amino acids, (d) polymers, (e) amines, and (f) miscellaneous along the NSTEC. The representatives of different colors were showed in Figure 2.

Fig.4. Redundancy analysis (RDA) ordination biplot of soil microbial carbon sources use efficiency and environmental properties. The representatives of different colors were showed in Figure 2. The dotted lines and solid lines represent the environmental variables and lipid signatures and carbon sources. The abbreviations of the variables in this figure are as follows: MAP, mean annual precipitation. The vegetation data: LDMC, leaf dry matter weight; Leaf C, leaf carbon content; Leaf N, leaf nitrogen content; SLA, specific leaf area. Soil properties included SMC, soil moisture content; Silt, soil silt content; TN, soil total nitrogen; SOC, soil organic carbon. The abbreviations of the sampling sites were given in Table 1

Fig.5. The heatmap of the Pearson's correlation coefficients between the use of individual substrates and microbial PLFAs and soil enzyme activities. Note: The abbreviations of the variables: Actino-, actinomycetes; F/B, fungi/bacteria; G^+, gram positive bacteria; G^-, gram negative bacteria; G^+/G^-, Gram-positive bacteria/ Gram-negative bacteria. BG, β-1, 4-glucosidase; NAG, β-1,4-N-acetylglucosaminidase; LAP, leucine aminopeptidase; AP, acid phosphatase. $^{**}P< 0.01$, $^{*}P< 0.05$.

Fig. 6. Relationships between soil carbon mineralization rates (μg C $g^{-1}d^{-1}$) and microbial biomass C (MBC), soil dissolved organic C (DOC), average well color development (AWCD), and individual substrate use.

Fig. 7. Relationships between soil carbon mineralization rates (μg C g^{-1} d^{-1}) and different groups of soil microbial PLFAs (a-h) and enzyme activities (i-l).

Supporting information

Table S1 Average values of forest soil enzyme activities and different PLFA groups along the NSTEC.

Table S2 Plant diversity and community weighted means of plant functional traits

Table S3 Soil organic matter (SOM) decomposition rates during the28 days of incubation time (Mean±SE) (μg C g^{-1} d^{-1})

Fig. S1 Variations in the average well color development (AWCD) values during a 240-h incubation for the nine forests. The abbreviations of the sampling sites are the same as those in Table 1.

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Tables

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] (ºC)	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

a:HZ, Huzhong; LS, Liangshui; CB, Changbai; DL, Dongling; TY,Taiyue; SN, Shennong; JL, Jiulian; DH, Dinghu; JF, Jiangfeng.
b: MAT, mean annual temperature; MAP, mean annual precipitation.

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

Sampling site	pH	ST (℃)	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

622 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
623 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.

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624 **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

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

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Figures

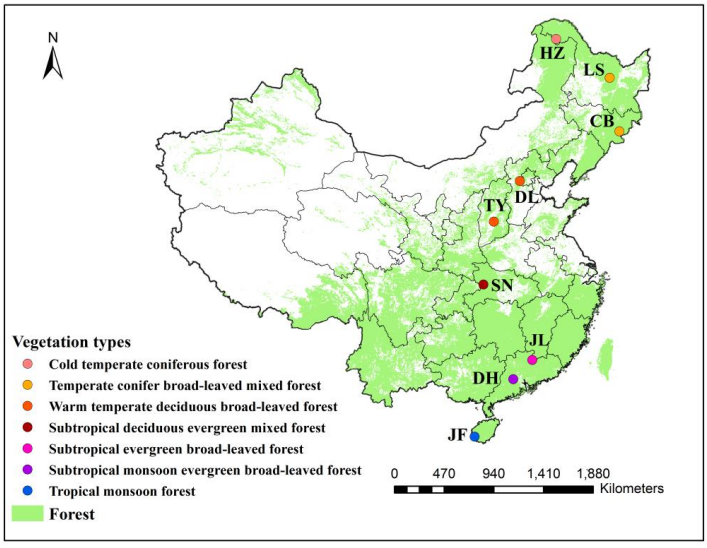

Figure 1. Distribution of typical forest ecosystems along the North-South Transect of eastern China (NSTEC). The abbreviations of sampling sites from north to south are as follows: HZ, Huzhong; LS, Liangshui; CB, Changbai; DL, Dongling; TY, Taiyue; SN, Shennong; JL, Jiulian; DH, Dinghu; JF, Jiangfeng.

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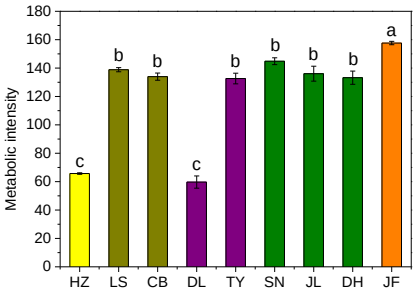

Figure 2. Variations in soil microbial substrate use during a 240-h incubation for the nine forests. Different colors represent different forest types: Yellow, coniferous forest; Dark yellow, coniferous broad-leaved mixed forest; Purple, deciduous broad-leaved forest; Olive, subtropical evergreen broad-leaved forest; Orange, Tropical monsoon forest. Different lowercase letters indicate significant differences among forests in the same climate zone. The abbreviations of the sampling sites are given in Table 1.

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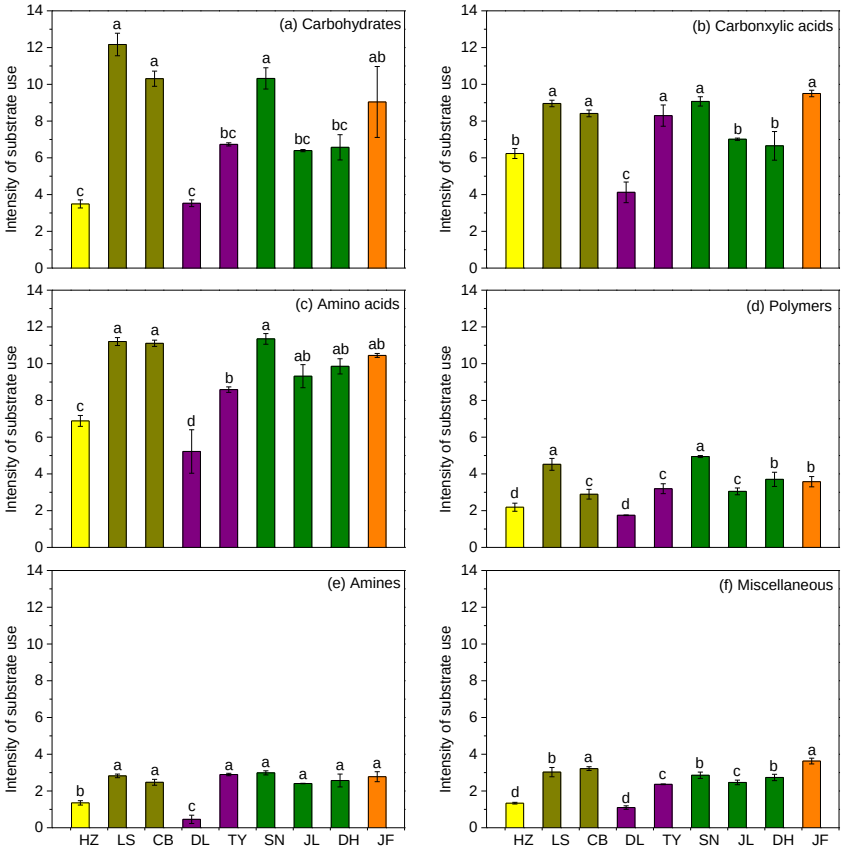

Figure 3. Characteristics of microbial use of (a) carbohydrates, (b) carboxylic acids, (c) amino acids, (d) polymers, (e) amines, and (f) miscellaneous along the NSTEC. The representatives of different colors were showed in Figure 2.

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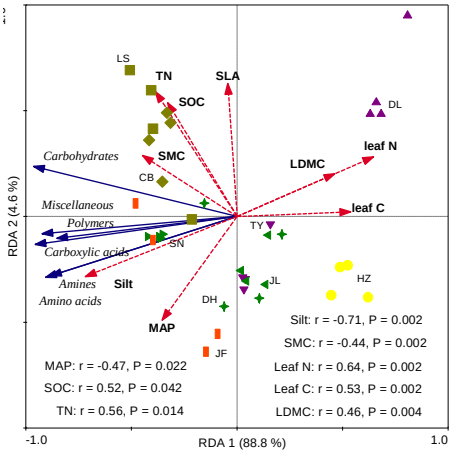

Figure 4. Redundancy analysis (RDA) ordination biplot of soil microbial carbon sources use efficiency and environmental properties. The representatives of different colors were showed in Figure 2. The dotted lines and solid lines represent the environmental variables and lipid signatures and carbon sources. The abbreviations of the variables in this figure are as follows: MAP, mean annual precipitation. The vegetation data: LDMC, leaf dry matter weight; Leaf C, leaf carbon content; Leaf N, leaf nitrogen content; SLA, specific leaf area. Soil properties included SMC, soil moisture content; Silt, soil silt content; TN, soil total nitrogen; SOC, soil organic carbon. The abbreviations of the sampling sites were given in Table 1.

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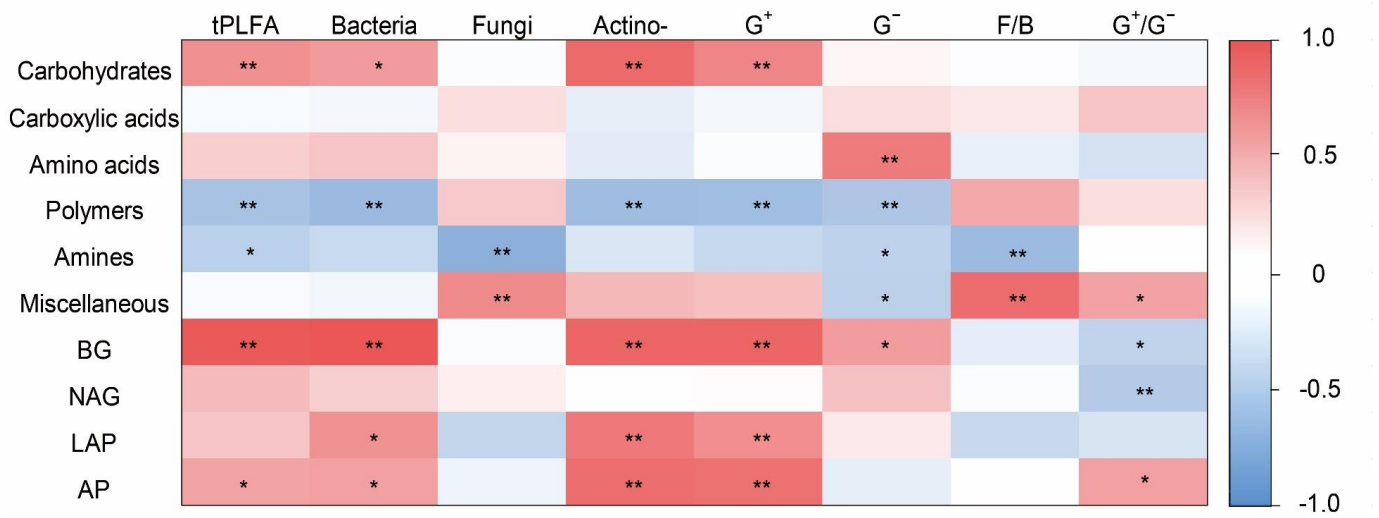

Figure 5. The heatmap of the Pearson's correlation coefficients between the use of individual substrates and microbial PLFAs and soil enzyme activities. Note: The abbreviations of the variables: Actino-, actinomycetes; F/B, fungi/bacteria; G^+, gram positive bacteria; G^-, gram negative bacteria; G^+/G^-, Gram-positive bacteria/ Gram-negative bacteria. BG, β-1, 4-glucosidase; NAG, β-1,4-N-acetylglucosaminidase; LAP, leucine aminopeptidase; AP, acid phosphatase. $^{**}P< 0.01$, $^{*}P< 0.05$.

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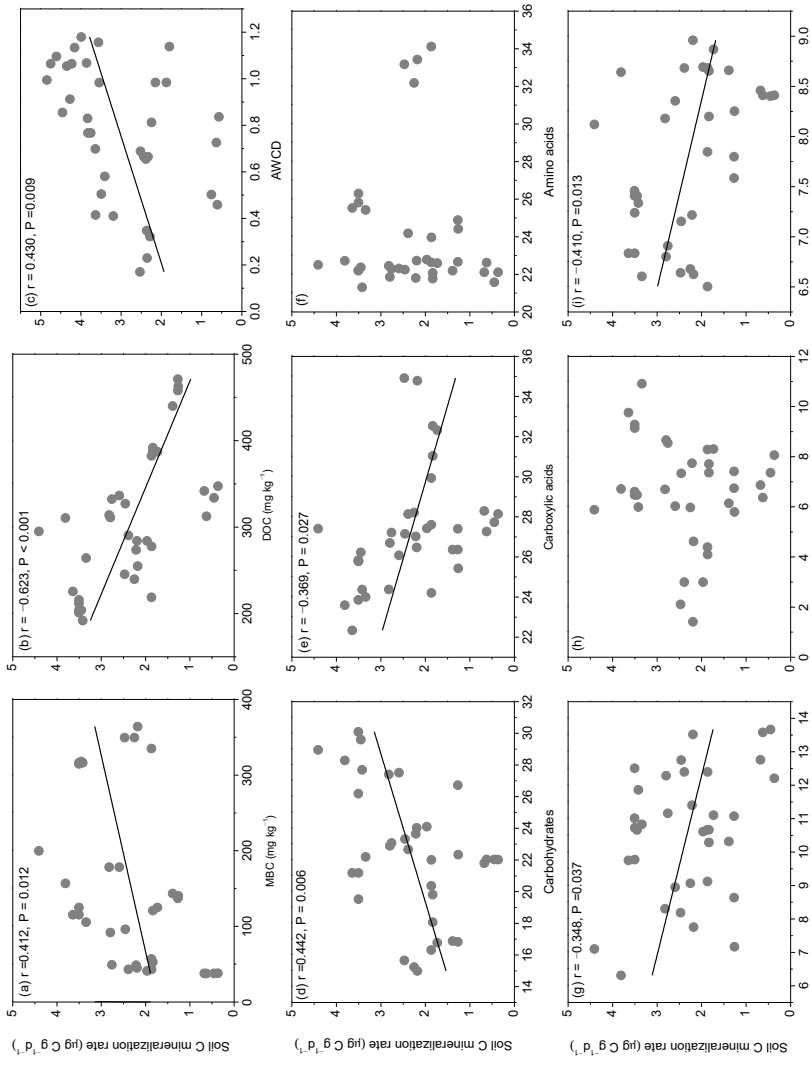

Figure 6. Relationships between soil carbon mineralization rates (μg C g^{-1} d^{-1}) and microbial biomass C (MBC), soil dissolved organic C (DOC), average well color development (AWCD), and use of individual substrates.

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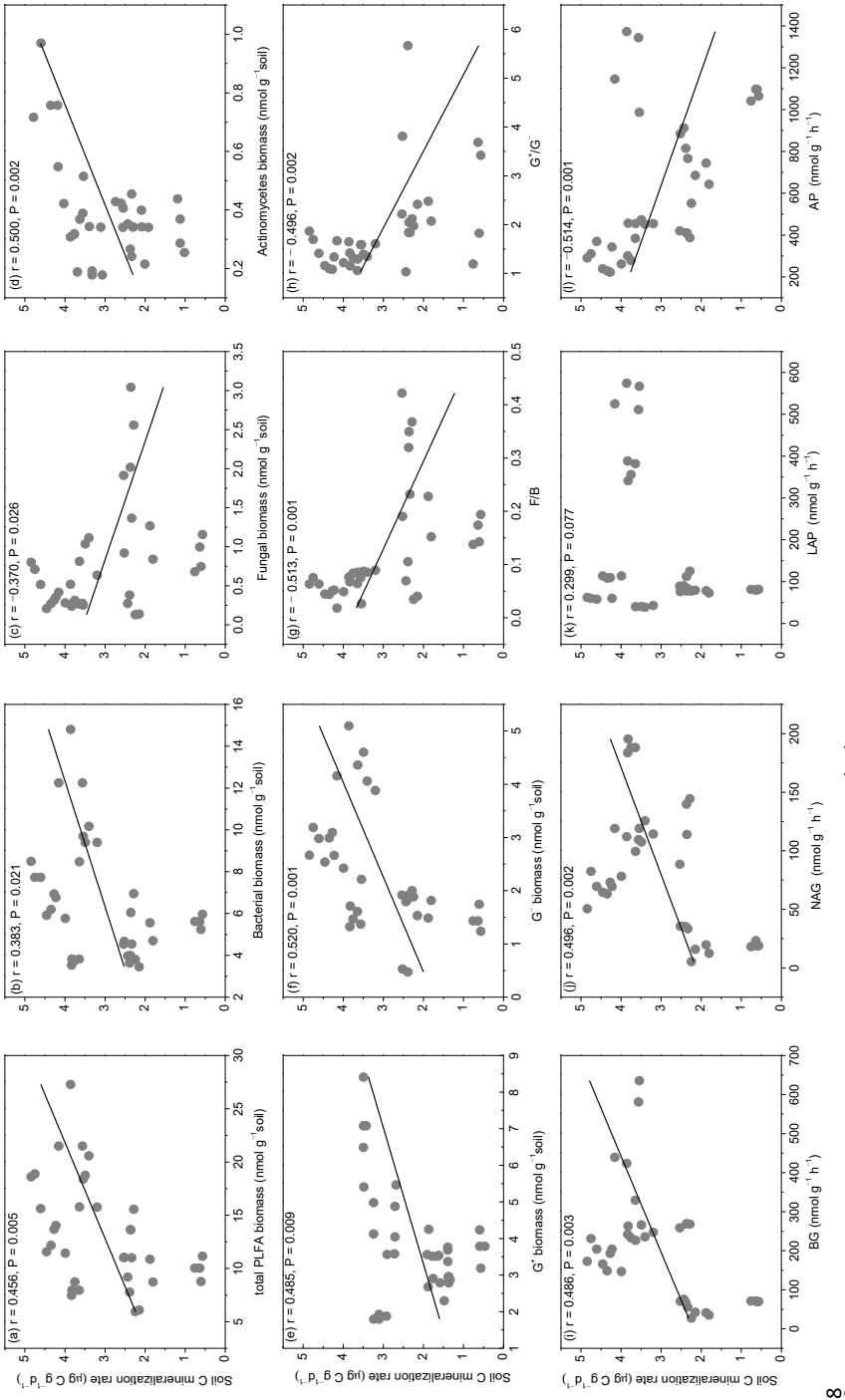

Figure 7. Relationships between soil carbon mineralization rates (μg C g^{-1} d^{-1}) and different groups of soil microbial PLFAs (a-h) and enzyme activities (i-l).