Plant functional traits determine latitudinal variations in soil microbial function: evidence from forests 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 latitudinal variation in the profiles of different substrate use along the NSTEC. Specifically, we found that the substrate use by microorganisms was highest in the temperate forest soils (intensities of 10–12), followed by the subtropical forest soils (intensities of 7–10), and was least in the coniferous forest soils (intensities of 4–7). The latitudinal variation in soil microbial function was more closely related to plant functional traits (P=0.002) than climate (P=0.022). The soil silt, leaf dry matter, and leaf C and N contents were the main controls on the biogeographical patterns of microbial substrate use in these forest soils. 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 actinomycic PLFAs, while the use of amine and miscellaneous substrates were related to soil G^- bacterial and fungal PLFAs. The enzyme production varied with changes in the soil microbial communities. The soil enzyme activities were positively correlated with the bacterial PLFAs but were not correlated with the fungal PLFAs. The soil organic matter (SOM) decomposition rates were significantly higher in the temperate forests than in the subtropical and tropical forests, emphasizing the rapid degradability of high-energy substrates, such as soil microbial biomass carbon, carbohydrates, and amino acids. The SOM decomposition rates were significantly and negatively related to soil dissolved organic carbon concentrations, carboxylic acids, polymers, and miscellaneous substrate use. The relationships between soil PLFAs and microbial substrate use, enzyme activities, and SOM decomposition rate show that, as the soil microbial community structure changes, soil biogeochemical processes also change.

Abbreviations

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

Soil microbial community

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

Soil enzyme activities

BG	β-glucosidase
NAG	N-acetylglucosaminidase
AP	Acid phosphatase
LAP	Leucine aminopeptidase

Soil properties

SMC	Soil moisture content
SOM	Soil organic matter
SOC	Soil organic carbon
TN	Total Nitrogen
DOC	Dissolved organic carbon
MBC	Microbial biomass carbon
Silt	Soil silt fractions (<53 μm)

Plant functional properties:

CWM	Community-weighted means
SLA	The specific leaf area
LDMC	Leaf dry matter content
Leaf C	Leaf C concentrations
Leaf N	Leaf N concentrations

1 Introduction

The catabolic diversity of soil microbial communities is a useful indicator of how microbial functions adapt to environmental stress. It can be used to test fundamental questions about soil biological resistance and resilience (Jagadamma et al., 2014; Swallow and Quideau, 2015), and help us 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 communities over large spatial scales.

Numerous studies have documented how environmental and anthropogenic perturbations impact on the structure, diversity (Tu et al., 2016; Zhou et al., 2016), and enzyme activities (Peng and Wang, 2016; Xu et al., 2017) of soil microbial communities, and have reported that 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, Tian et al. (2015), from their study of Changbai Mountain, China, found that the soil microbial metabolic activity and functional diversity were spatially dependent. Others reported that soil microbial activities varied by forest type, 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). The soil microbial metabolic abilities are also influenced by the dominant tree species, through the production of chemically-unique litter and root exudates, and the soil physico-chemical properties (Menyailo et al., 2002). 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 in soil microbial

activities mainly reflect the climate, soil pH, and total phosphorus concentrations over large geographic scales (Cao 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 gram positive bacteria (G^+) were mainly responsible for the decomposition of pine needles and soil organic matter, but gram negative bacteria (G^-) 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). Research to date suggests that the different microbial communities will result in variations in soil microbial function and soil biochemical processes, so information about the relationships between soil microbial communities and their functions in natural ecosystems is 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 large-scale geographical patterns in microbial communities and their responses to environmental changes. 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 four hypotheses in this study, as follows: (1) The profiles of soil microbial substrate use vary along a latitudinal gradient, (2) the functional characteristics of soil microbes are similar in closely related forest types, (3) biogeographical patterns of soil microbial substrate use are constrained by climate and plant functional traits, and (4) different soil microbial communities may have substrate use profiles and SOM decomposition rates.

2 Material and methods

2.1 Study area and soil sampling

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

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

2.2 Soil chemical analyses

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

analysis and PLFAs are expressed in units of nmol g^{-1}. The four enzymatic activities of β-glucosidase (BG), N-acetylglucosaminidase (NAG), acid phosphatase (AP), and leucine aminopeptidase (LAP) responsible for soil C, N, and phosphorous cycling, were measured following the procedure outlined 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.

The Biolog-ECO plates were purchased from Biolog, US. The substrates for BG, NAG, AP, and LAP were 4-MUB-β-D-glucoside, 4-MUB-N-acetyl-b-D-glucosaminide, 4-MUB-phosphate, and L-Leucine-7-amino-4-methylcoumarin, and were stored at −20 °C. An MUB standard was used for the BG, NAG, and AP enzymes and an AMC standard was used for the LAP enzyme. The substrates and standards were purchased Sigma. Analytical grade reagents were used for the soil nutrient analysis.

2.3 Vegetation data

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

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

Where P_i was the importance value of the species i as a proportion of all species, and n was the number of the species.

We also calculated the community-weighted means (CWM) values of the tree traits using the cover of each tree. 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. To measure the leaf traits at the community level, we calculated the CWM of the

tree layer, as follows:

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

Where *pi* is the relative contribution of the species *i* to the cover of the whole community, *n* is the number of the most abundant species, and trait $_i$ is the trait value of species *i*, 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):

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

Where v_i was the 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 the 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

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

Of the forests along the NSTEC, the C metabolic intensity of soil microbes was lowest in HZ and LS; the C metabolic intensity of soil microbes differed significantly between JF and the other forests (Fig. 2), which indicates that the color development was significantly higher in the tropical forest soils than in the subtropical and temperate forest soils and is consistent with the variations in the AWCD

(Fig. S1). The average values of *R*, *H'*, and *D* were significantly different among the nine forest soils and were highest in JF, SN, and CB (Table 3).

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

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

3.2 Effect of environmental properties on soil microbial substrate use

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

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 the 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 than closer to the tropics (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 Mechanisms driving latitudinal variations 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 carbon substrate use was lowest in the coniferous forest. This shows that, compared with coniferous species, broadleaved tree species produce root exudates and litter high in water-soluble sugars, organic acids, and amino acids that are more favorable for microbial activity (Priha et al. 2001). There was no significant latitudinal pattern in the C metabolic intensity of soil microbes in our study, which was inconsistent with hypothesis (1). Our results show that MAP only had a moderate effect on the soil microbial function (Fig. 4). However, there was significant spatial variation in the use of different carbon sources, which was also related, to a lesser extent, to climate. Consistent with hypothesis (2),

355 soil microbial functions were similar in closely related tree species and diverged as the variability
356 between tree species and forest types increased (Fig. 4), which suggests that plant traits have more
357 influence on soil microbial functions than climate.

358 A growing number of studies reported that vegetation type, land use, soil nutrients, and soil
359 organic matter quality and quantity can determine large scale patterns of microbial communities (de
360 Vries et al., 2012; Tu et al., 2016). Plant functional traits that are related to growth may determine a
361 tree species' ability to contribute to the soil carbon pool via leaf litter inputs. For example, it was
362 previously reported that plant traits such as the leaf N content, SLA, and LDMC could explain
363 variations in soil nutrients and litter decomposition rates (Eichenberg et al., 2014; Laughlin, 2011).
364 Therefore, we examined how these plant traits influenced the soil microbial function by latitude. We
365 found that changes in the soil microbial C substrate use with latitude were mainly related to the soil
366 silt contents and the CWMs of LDMC, and leaf C and leaf N concentrations, which indicates that the
367 quality of nutrients from plants had a major influence on microbial carbon use efficiency (Hypothesis
368 (3)). Plant species with high a SLA, high leaf N concentrations, and low LDMC can produce
369 bacterial-dominated soil microbial communities in grasslands (Orwin et al., 2010). Looking beyond
370 individual traits, related tree species may cultivate microbial communities with similar preferences
371 for carbon sources through coevolution of plants and microbes (Liu et al., 2012b; Buscot, 2015).

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

383 We also found that the C substrate use was negatively correlated with the CWM of leaf C

384 concentrations (Table S2, Fig. S2). Plants at high latitudes may have higher leaf C concentrations
385 than plants at lower latitudes so that they can balance the osmotic pressure of cells and resist freezing
386 (Millard et al., 2007; Hoch and Körner, 2012). The increased C was most likely in the form of an
387 increase in non-structural C, including starch, low molecular weight sugars, and storage lipids that
388 are easy to break down. Therefore, soil microorganisms from the temperate forests mainly
389 metabolized high-energy substrates, such as carbohydrates, carboxylic acids, and amino acids.

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

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

409 4.3 Links between soil microbial community structure and function

410 The soil microbial community structure and functions were significantly correlated along the NSTEC.
411 Soil carbohydrate and polymer substrate use were mainly related to soil G^+ bacterial and actinomycic

412 biomass, but amines and miscellaneous substrates were mainly related to soil G^- bacterial, fungal
413 biomass, and the F/B ratio. Soil bacteria mainly decomposed simple carbohydrates, organic acids,
414 and amino acids, whereas soil fungi mainly decomposed recalcitrant compounds (Myers et al., 2001;
415 Treonis et al., 2004). Consistent with this, soil bacterial PLFAs were positively correlated with the
416 carbohydrate substrate use and the fungal PLFAs were positively related with miscellaneous substrate
417 use. The results are similar to those reported by Sterner and Elser (2002), who found that fungi tended
418 to have higher C/N or C/P ratios while heterotrophic bacteria typically have lower C/N or C/P ratios.
419 Shifts in microbial community composition may influence enzyme production (DeForest et al.,
420 2012; Waldrop et al., 2000; Brockett et al., 2012). Different microbial groups require different
421 amounts of nutrients to construct biomass, or have enzymes that differ in their affinity for nutrients.
422 We found that the relative abundances of the G^+ bacteria and actinomycetes communities were
423 associated with the specific activities of BG, AP, and LAP), whereas the relative abundance of the
424 G^- bacteria was correlated with soil NAG activities involved in chitin degradation. In agreement with
425 our study, numerous other researchers have reported significant correlations between PLFA profiles
426 and enzyme activities (Waldrop et al., 2000; DeForest et al., 2012; Brockett et al., 2012; Riah-Anglet
427 et al., 2015). Soil BG was mainly responsible for cellulose degradation and was involved in breaking
428 down complex organic compounds (cellobiose) into small molecule substrates (glucose) in favor of
429 acquiring C through microbial community growth (Waldrop et al., 2000). Soil NAG activities were
430 weakly and positively related with fungal biomass in the present study, and may have been mainly
431 produced by fungal populations (Valášková et al., 2007). Fungi are commonly considered as
432 producers of oxidative enzymes. Therefore, the influence of fungal biomass on variations in enzyme
433 activities was minimal (Kivlin and Treseder, 2014). The linkages between enzyme activity and
434 community composition may provide some insight into the microbial mechanisms that drive the
435 decomposition of macromolecular C compounds. These results suggest that that overall ecosystem
436 functioning may suffer if soil microbial groups are lost.
437 The quality and amounts of SOM are influenced by the biomass, vegetation coverage, root
438 distribution, and microbial species (Raich and Schlesinger, 1992). The SOM decomposition rates
439 were higher in temperate forests than in tropical forests and may reflect the higher soil microbial
440 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, carboxylic acids, polymers, and miscellaneous along the NSTEC, indicate a shift in the soil C turnover from open to closed with increases in the soil labile C concentrations (Fang et al., 2014). Soil DOC and MBC influence SOM decomposition rates indirectly by regulating microbial properties (Boberg et al., 2014; Wei et al., 2014). In our study, SOM decomposition rates were positively related with bacterial PLFAs but negatively with fungal PLFAs. 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 microbial activities and the decomposition rates of organic matter (Lipson et al., 2009; Keiblinger et al., 2010). The functional dissimilarity of microbes and fungi may help explain these results. However, we did not measure some key variables, such as the microbial competition and interactions, and relationship between the microbial diversity and the decomposition rates. Therefore, in the future, we will use different experimental techniques that will help us gain an improved understanding of the mechanisms that drive the relationships between the structure and function of microbial communities.

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 suggests that the loss of soil microbial groups may have consequences for overall ecosystem functioning.

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., Q.F.W., and Z.P.L. 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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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.

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.

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

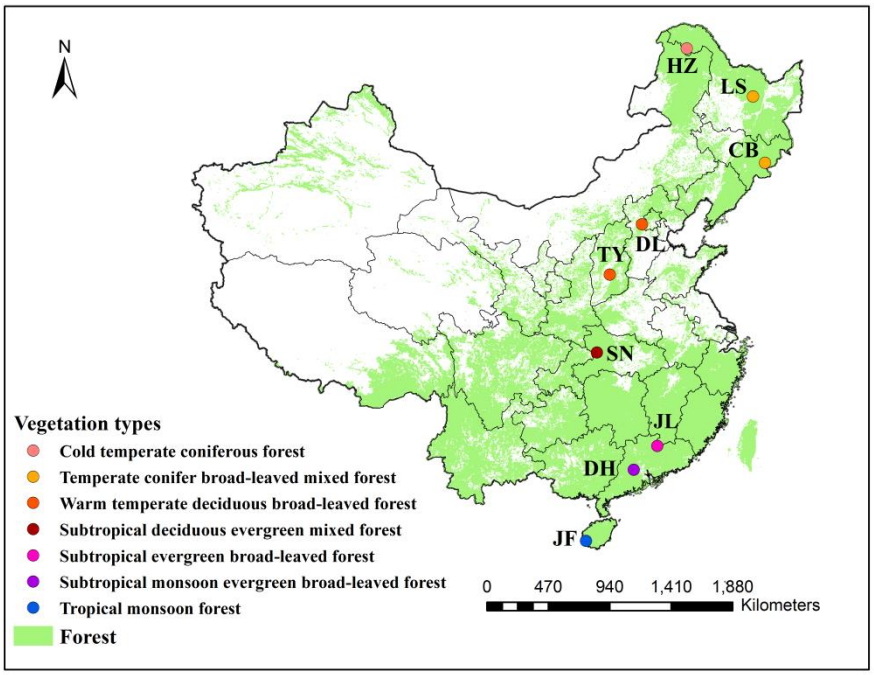
Note: ST=temperature of 0–10 cm soil; SMC=soil moisture content; Silt=soil silt content; SOC=soil organic carbon; MBC=microbial biomass carbon; DOC=dissolved organic carbon; TN=soil total nitrogen; TP=soil total phosphorus. Values were presented as means ± SE (n=4). The abbreviations of the sampling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

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

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

712 # Figures



713 **Figure 1.** Distribution of typical forest ecosystems along the North-South Transect of eastern China (NSTEC).
714 The abbreviations of sampling sites from north to south are as follows: HZ, Huzhong; LS, Liangshui; CB,
715 Changbai; DL, Dongling; TY, Taiyue; SN, Shennong; JL, Jiulian; DH, Dinghu; JF, Jiangfeng.
716

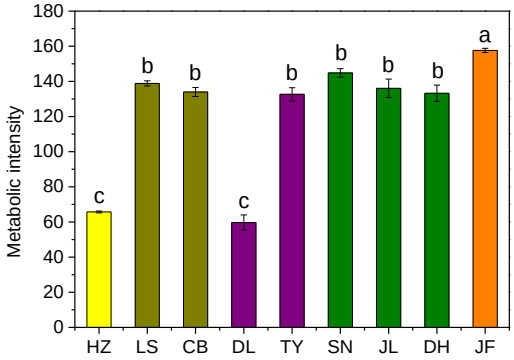


Figure 2. Variations in soil microbial substrate use during a 240-h incubation for the nine forests. Different colors represent different forest types: Yellow, coniferous forest; Dark yellow, coniferous broad-leaved mixed forest; Purple, deciduous broad-leaved forest; Olive, subtropical evergreen broad-leaved 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.

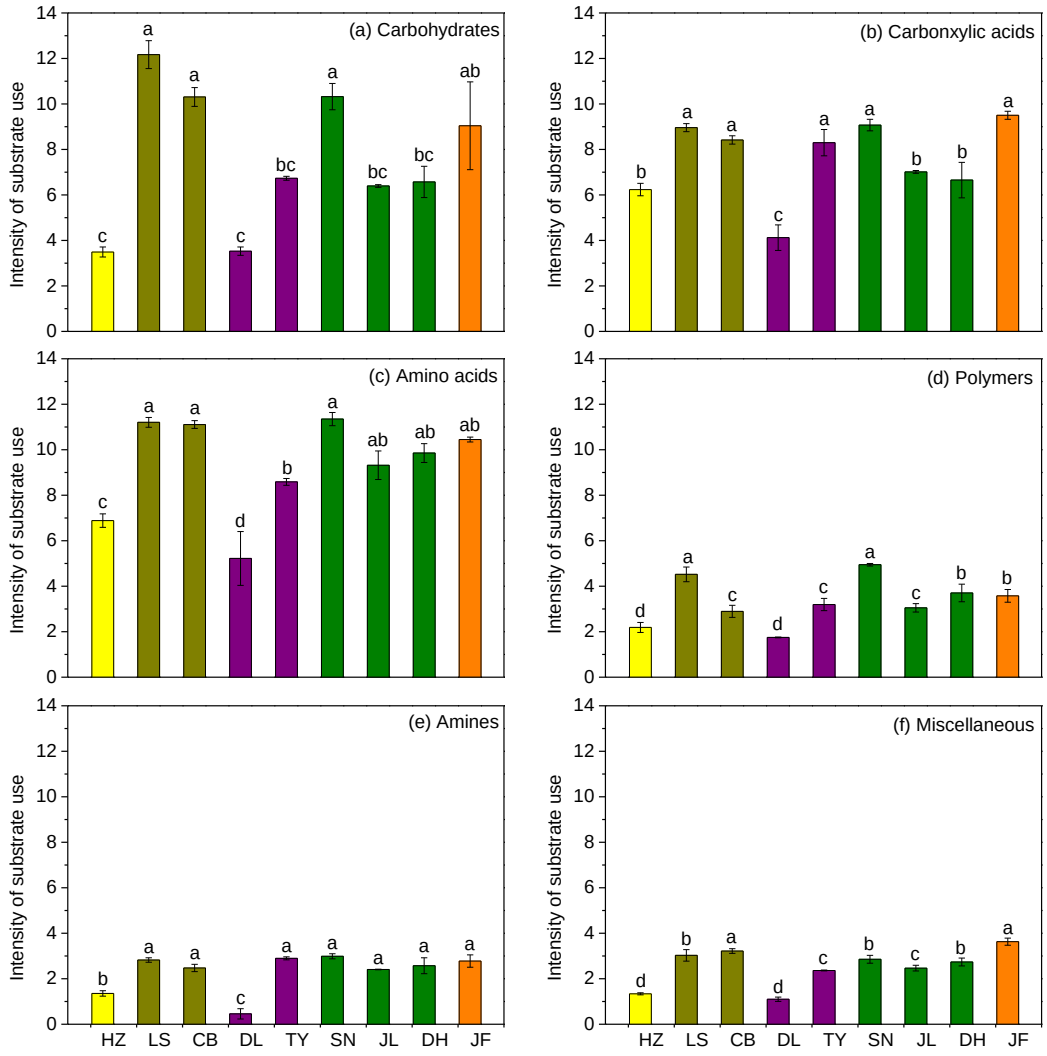


Figure 3. Characteristics of microbial use of (a) carbohydrates, (b) carboxylic acids, (c) amino acids, (d) polymers, (e) amines, and (f) miscellaneous along the NSTEC. The representatives of different colors were showed in Figure 2.

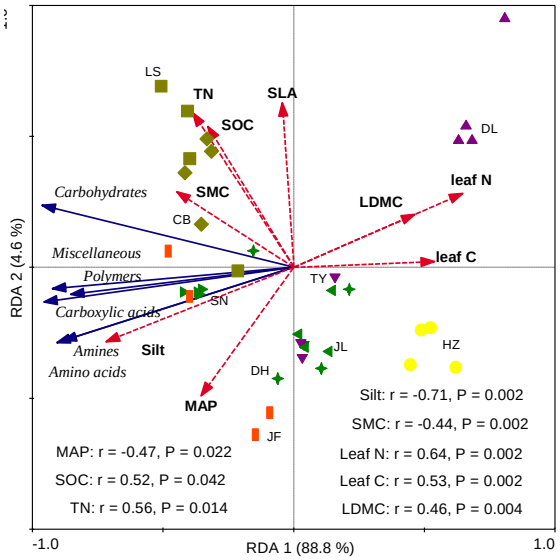


Figure 4. Redundancy analysis (RDA) ordination biplot of soil microbial carbon sources use efficiency and environmental properties. The representatives of different colors were showed in Figure 2. The dotted lines and solid lines represent the environmental variables and lipid signatures and carbon sources. 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.

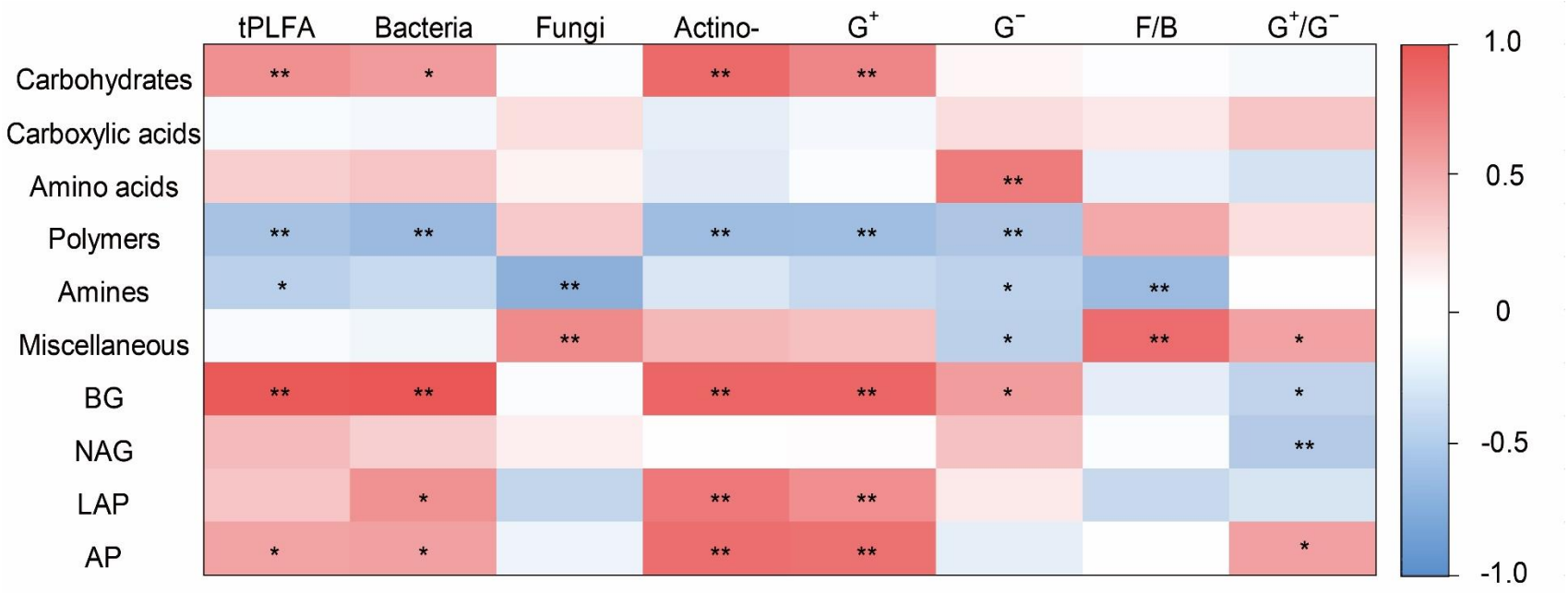


Figure 5. The heatmap of the Pearson's correlation coefficients between the use of individual substrates and microbial PLFAs and soil enzyme activities. Note: The abbreviations of the variables: Actino-, actinomycetes; F/B, fungi/bacteria; G^+, gram positive bacteria; G^-, gram negative bacteria; G^+/G^-,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

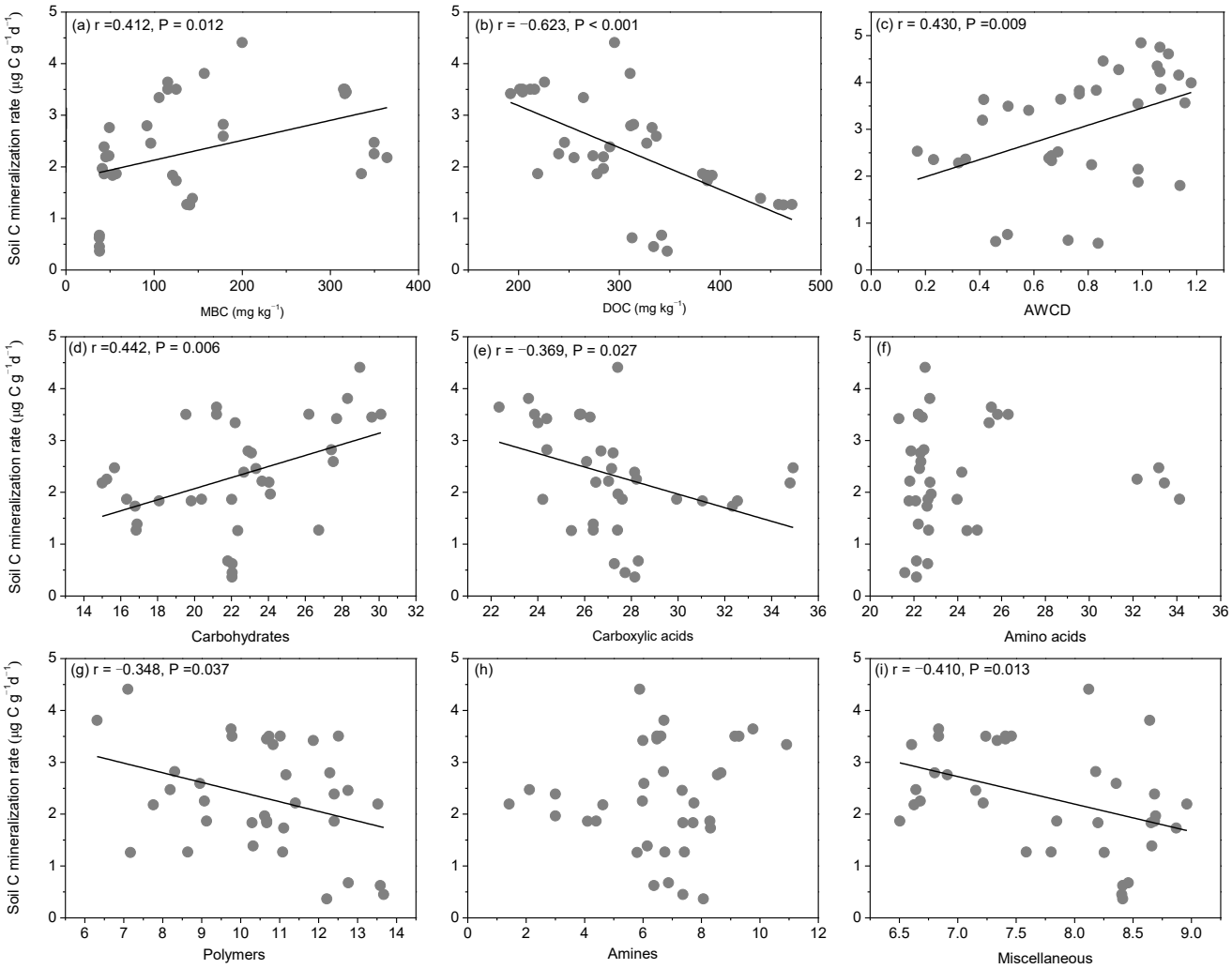


Figure 6. Relationships between soil carbon mineralization rates (μg C g^{-1} d^{-1}) and microbial biomass C (MBC), soil dissolved organic C (DOC), average well color development (AWCD), and use of individual substrates.

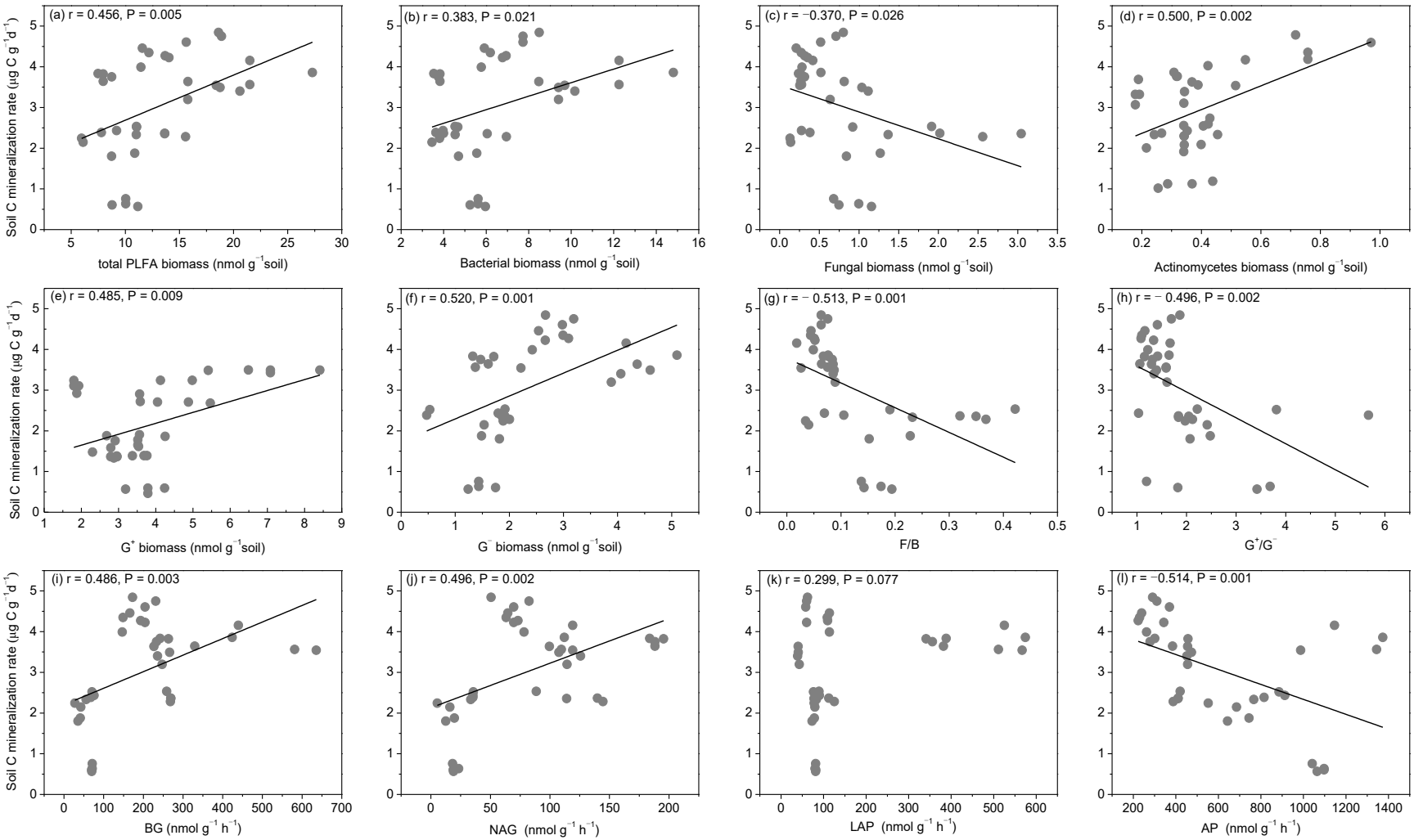


Figure 7. Relationships between soil carbon mineralization rates (μg C g^{-1} d^{-1}) and different groups of soil microbial PLFAs (a-h) and enzyme activities (i-l).