

# Traits of dominant species and soil properties co -regulate soil microbial communities across land restoration types in a subtropical plateau region of Southwest China

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1	Traits of dominant species and soil properties co-regulate soil microbial T communities across land
2	restoration types in a subtropical plateau region of Southwest China
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10	Keywords: Plant functional traits, Soil microbial community, Mass-ratio hypothesis, Soil properties
11	Abstract
12	Soil microbial community is essential for maintaining and improving ecosystem functioning in
13	ecological re-storation practice and is intimately linked with the plant community. However, little is
14	known on how soil microbial communities respond to the functional characteristics of plant
15	communities. Here we investigated the changes in plant community functional attributes, soil
16	properties, and soil microbial community characteristics of four land restoration (vegetation) types
17	in a subtropical plateau region. The relative contributions of soil abiotic properties and plant
18	community functional attributes to variation in microbial community composition and function were
19	then assessed. We found that plant community attributes, soil properties, and the soil mi-crobial
20	communities differed significantly among land restoration types, and the plant functional traits of
21	dominant species and soil properties jointly determined soil microbial community structure and
22	functions. Specifically, soil microbial community structure was significantly linked to the community-
23	weighted mean (CWM) of plant functional traits, soil water content, and soil organic carbon. Soil

24 microbial carbon-metabolic functions were tightly correlated with the CWM of leaf dry matter 25 content, specific leaf area, and specific root length. Variance partitioning also revealed that the 26 CWM of plant functional traits and soil variables co-operatively explained 67% and 64% variation in 27 soil microbial community structure and carbon-metabolic functions. Meanwhile, significant 28 correlations were found between variation in microbial community compo-sition and carbon-29 metabolic functions. In conclusion, our observations demonstrate that soil microbial com-munity 30 characteristics were governed by dominant species in plant communities across land restoration 31 types, mainly due to differences in plant functional traits and soil resource driven by plant traits.

32

## 33 1. Introduction

34 Biodiversity has been considered the key determinant of changes in ecosystem processes and 35 functions (Hooper et al., 2005). Some studies have reported that the species diversity of an 36 aboveground community may affect the soil functions via changes in soil biological and physi-37 cochemical properties (Landesman et al., 2014; Lladó et al., 2018). However, an increasing focus of 38 research is devoted to the functional characteristics of organisms, exploring how changes in 39 functional di-versity influence soil functions and their response to environmental change (Bardgett, 40 2017; Faucon et al., 2017; Grigulis et al., 2013; Lavorel et al., 2013). Further, trait-based approaches 41 are being used to predict how changes in vegetation composition influence soil properties and processes (Bardgett, 2017; De Deyn et al., 2008; Grigulis et al., 2013). Soil microbial community, as a 42 43 major driver of soil biogeo-chemical cycles, soil formation, and ecosystem resilience to the external 44 environment, is important to soil properties and processes (Khlifa et al., 2017; Wardle et al., 2004). 45 However, the effects of functional plant traits and their diversity on soil microbial communities are 46 far from being fully understood.

48 Changes in soil microbial community composition are not only in-fluenced by soil physicochemical 49 factors such as pH, soil organic carbon (SOC), and nutrient availability (Landesman et al., 2014; Lladó 50 et al., 2018) but also by plant properties such as plant community type, plant-microbial interactions, 51 and plant functional traits (Bauhus and Paré, 1998; de Vries et al., 2012; Pei et al., 2016). Scheibe et 52 al. (2015) de-monstrated that tree species identity and site conditions were more important factors 53 in determining the soil microbial community struc-ture than tree species diversity. It has been 54 proposed that plant leaf economics spectrum could provide a framework for understanding how 55 vegetation composition influences variation in soil microbial commu-nities (Wardle et al., 2004). The 56 general idea is that plant species with a higher specific leaf area (SLA) and a lower leaf dry matter 57 content (LDMC) can shape the bacteria-dominated soil microbial communities. In contrast, plant 58 species with low SLA promote the growth of fungi relative to bacteria (Orwin et al., 2010; Wardle et 59 al., 2004). However, these studies measured only plant attributes on the species scale and did not 60 consider functional characteristics on the community scale. Therefore, we do not understand how 61 soil microbial communities re-sponse to changes in the functional diversity of the plant community.

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63 Functional diversity of plant community describes the distribution of species in functional trait space 64 and is hypothesized as being bene-ficial for ecosystem processes and functions (Mason et al., 2005). 65 At the community scale, the community-weighted means (CWM) of some functional traits (e.g., SLA, LDMC, or plant height), which describes the dominant functional trait value of a community and is 66 67 closely related to the mass ratio hypothesis, can respond to environmental change and affect soil 68 biological processes and nutrient cycling (Garnier et al., 2004). The mass ratio hypothesis proposes 69 that ecosystem functioning is primarily determined by the functional traits of the dominant species 70 and is frequently used to quantify the functional characteristics of plant communities (Lavorel et al., 71 2008). Simultaneously, soil microbial community may be modified by soil physicochemical properties 72 that are induced by changes in community functional attributes (De Deyn et al., 2008; Orwin et al.,

2010). Some studies of plant-soil interactions have confirmed that soil properties (e.g., pH, soil
moisture, soil organic carbon) play an important role in the interactions between plant species and
soil microbial communities (De Deyn et al., 2009; Harrison and Bardgett, 2010). Therefore, it is
plausible that plant community func-tional attributes and their effect on soil properties (such as soil
texture and nutrient resources) cooperatively shape the structure and functions of soil microbial
communities.

79

80 Concerns over the continuing loss of biodiversity and the associated decline of ecosystem functions 81 have triggered numerous studies aiming at developing more sustainable ecological protection and 82 restoration practices (Faucon et al., 2017). Many studies suggest that, compared with plant species 83 richness, plant functional traits and functional di-versity metrics can be used to evaluate functional 84 responses to re-storation projects (D'Astous et al., 2013; Laughlin, 2014; Zirbel et al., 2017). In the 85 subtropical plateau region of southwest China, different land restoration types including naturally 86 recover and establishing plantations have been widely adopted for maintaining soil fertility and 87 controlling soil and water loss. For example, plantation forest with Eucalyptus or Pinus species is 88 considered as one of the main forms of land restoration due to their attributes of fast growth and 89 industrial production of wood, oil, and fuel. At the same time, natural regenera-tion has also proved 90 to be another effective approach to land restoration in this area (Fu et al., 2018). Although previous 91 studies have shown that different vegetation restoration methods influence plant community composition, soil nutrients, and ecosystem functions (e.g. water and soil conservation) (Fu et al., 92 93 2009, 2018; Hou et al., 2010), little is known on how soil microbial communities respond to the 94 functional char-acteristics of plant communities in this region.

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97 In this study we investigated changes of soil microbial community composition and carbon-98 metabolic function in different land restoration types using phospholipid fatty acid analysis (PLFA) 99 and community-level physiological profiles (CLPP), respectively, and then evaluated the relative 100 effects of plant community attributes and soil physicochemical properties on soil microbial 101 communities. We hypothesized that (1) soil microbial community composition and carbon-metabolic 102 functions differ between the different land restoration types; (2) soil microbial communities are 103 significantly driven mainly by changes in the plant community-weighted means of functional traits 104 the functional traits and soil physicochemical properties.

105 2. Material and methods

106 2.1. Study area

107 The study area is located at Jiulongdian catchment (257.6 km2) in Mouding County (25°24'09" N, 108 101°28'18" E), mid-Yunnan, SW China. The average annual rainfall in the area, which lies in the 109 subtropical monsoon climate zone, is 846 mm, and the rainy season lasts from May to October each 110 year. The average annual temperature is 16 °C. The soil of the area is Cambisols (according to 111 FAO/UNESCO classifications). The original vegetation in this region was a subtropical evergreen 112 broad-leaved forest, most of which was utilized as coppices for fuel-wood or pastures. Since the 113 1980s, some of these have been planted by fast-growing Pinus yunnanensis after deforestation. 114 Other remnant cop-pices and pastures were abandoned and formed different secondary stands after natural regeneration. 115

Currently, this area represents sections of different vegetation in-cluding secondary shrubland (SL),
coniferous forest (CF), semi-natural forest (SNF), and natural secondary forest (NSF) (Tang et al.,
2010). These four land restoration types are described as follows: (1) SL, the land has been closed for
at least 15 years since the last domestic live-stock grazing and repeated cutting; (2) CF, the manmade plantation is dominated by the coniferous species P. yunnanensis with a history of aerial

planting on abandoned lands followed by the closing of the land for reforestation; (3) SNF, mixed
needle-broad leaved forest dominated by P. yunnanensis and Keteleerla evekyniana with a history of
clear-cut-ting followed by a period of approximately 45 years of forest reserva-tion; and (4) NSF,
dominated by Cyclobalanopsis glaucoldes and K. eve-kyniana and reserved without any interruption
for a period of approximately 55 years.

126 2.2. Investigation and sampling procedures

127 In July and August 2018, we selected three representative sites with four vegetation restoration 128 types in this catchment. The sites are located at Samachang (25°14'35″ N, 101°27'12″ E, app. 2050 129 m.a.s.l.), Huafoshan (25°18'48" N, 101°25'12" E, app. 2340 m.a.s.l.), and Ximiji (25°15'23" N, 130 101°25′23″ E, app. 2010 m.a.s.l.). The distance between the sites is greater than 2.5 km to reduce 131 the effects of spatial auto-correlation. In each site, we established a representative  $10 \times 10$  m plot 132 for each vegetation restoration type. The plot of one vegetation type is more than 200 m apart from 133 another vegetation type on the same site. All 12 plots belonged to the same climatic and soil zones 134 and have a similar slope direction (20–25° west of north) and gradient (15–17°). Plant species 135 diversity and community functional characteristics in each plot were firstly calculated based on the 136 investigation of plant community structure and estimation of plant functional traits for each species. 137 Second, ten soil cores from 0 to 10 cm were taken at random locations in each plot. These cores 138 were pooled and sieved (2 mm mesh) to eliminate rocks and stones. Each mixed sample was divided 139 into two subsamples: one was used to analyze basic soil physicochemical prop-erties; the other was 140 freeze-dried to analyze the soil microbial com-munity composition and functions. Additionally, 141 another three un-disturbed soil samples were collected by metal cylinders to measure soil water 142 content (SWC).

143 2.3. Plant community properties

144 For each plot, the abundance of a given species was determined based on the basal area or the 145 estimation of percent cover for plants < 1.5 cm DBH (details in Fu et al., 2018). In the analyses, a 146 total of 27 species were recorded and used to quantify species diversity (H, Shannon index; R, 147 richness; and E, evenness) and plant community functional attributes. Five important plant 148 functional traits: leaf dry matter content (LDMC), specific leaf area (SLA), leaf nitrogen con-149 centration (LNC), leaf phosphorus concentration (LPC), and specific root length (SRL) were selected 150 because these traits are closely corre-lated with plant potential relative growth rate, nutrient 151 quality, nu-trient acquisition strategy, and productivity (Cornelissen et al., 2003; Vile et al., 2006). 152 These traits were measured based on at least 5 in-dividuals of each species following standardized 153 protocols (Cornelissen et al., 2003), and the mean of each trait for each species was calculated and 154 then used to calculate the community functional attributes. The CWMs were used as the index of 155 functional diversity of plant commu-nity, which calculated for each trait and for every plot using the 156 mean species trait values and the species relative abundance (Garnier et al., 2004). The species 157 diversity and all the indices of community functional attributes were calculated using the FDiversity software package (Casanoves et al., 2011). 158

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## 161 2.4. Soil physicochemical properties

Soil physicochemical properties including pH, soil water content (SWC), soil organic carbon (SOC), total nitrogen (TN), and total phos-phorus (TP) were determined. Soil pH was measured in a 1:2.5 (soil to water ratio) mixture using a glass electrode. The SWC, SOC, TN, and TP were measured using the drying method, the potassium dichromate sulfuric acid oxidation, the semi-micro Kjeldahl, and the phosphomo-lybdate blue methods, respectively. All procedures for the determina-tion of soil physicochemical indices were based on the methods de-scribed in Gregorich and Carter (2007).

### 168 2.5. Soil microbial community analysis

169 The soil microbial community structure and carbon metabolic functions were characterized using 170 PLFAs and CLPPs. The PLFAs were extracted from 4 g of soil with a chloroform: methanol: phosphate 171 buffer mixture (1:2:0.8, v/v/v) following the procedure of Frostegård et al. (Frostegård et al., 1993). 172 The extracted lipids were eluted with chloroform, acetone, and methanol on solid-phase extraction 173 columns to obtain the phospholipids. The phospholipids were then subjected to mild alkaline 174 methanolysis, and the extractions were redissolved in hexane with an internal standard of 19:0. 175 Finally, the samples were analyzed using gas chromatography/mass spectrometry with the fol-176 lowing parameters: capillary column (HP-5), He as a carrier gas at a flow rate of 0.8 mL min-1, and 177 an injection volume of 1 µL. The abundance of individual PLFAs was expressed as nanomoles of 178 PLFAs per gram dry soil (nmol/g), and the total PLFAs was calculated as the sum of all PLFAs and 179 used a measure of microbial biomass. The dif-ferent PLFAs were considered to represent different 180 taxonomic groups: Gram-negative (G-) bacteria were represented by  $cy17:0, 16:1\omega7, 18:1\omega7$  and 181 cy19:0 (Zogg et al., 1997); Gram-positive bacteria (G+) were represented by i15:0, a15:0, i16:0, i17:0 182 and a17:0 (Moore-Kucera and Dick, 2008); fungal biomass was represented by 18:2w6,9 and 18:1w9 183 (Bååth and Anderson, 2003); actinomycete biomass was re-presented by 10Me16:0, 10Me17:0 and 184 10Me18:0 (Moore-Kucera and Dick, 2008); arbuscular mycorrhizal fungi (AMF) were represented by 185 16:1ω5c (Frostegård and Bååth, 1996); and 20:3ω6 and 20:4ω6 were assumed to represent 186 protozoans (Ringelberg et al., 1997). The struc-ture of the soil microbial community was also 187 characterized using the fungi:bacteria ratio (F:B) and the G+:G- ratio. 188 The capacity of soil microbial communities to utilize carbon sources was assessed with CLPPs using 189 Biolog EcoPlates (Biolog, Inc., USA). Each EcoPlate contained 31 different carbon sources, which

190 were di-vided into six groups: carboxylic acids, polymers, carbohydrates, phe-nolic acids, amino

acids, and amines. Soil suspensions were obtained according to the method described by Wu et al.

192 (2013) and were then inoculated into each well. The plates were incubated at 25 °C for 10 days, and

the color development in each well was recorded as the optical density at 590 nm with an
automated plate reader at regular 24 h intervals. Finally, the soil microbial activity in each
microplate was assessed as the average well color development (AWCD) as follows: AWCD =
5ODi/31, where ODi is the optical density value in each well.

197 2.6. Statistical analysis

198 Plant community characteristics (species diversity and CWM for each trait), soil physicochemical 199 properties, soil microbial community composition and carbon-metabolic functions (PLFAs and CLPPs, 200 re-spectively) under different land restoration types were compared using a one-way ANOVA and an 201 LSD test. We further used non-metric mul-tidimensional scaling (NMDs) based on the Bray-Curtis 202 index to vi-sualize the dissimilarity in soil microbial composition across plots. NMDs is an effective 203 method in community analysis because it does not assume linear distribution of the data (Pei et al., 204 2016). The significance of the variations in the composition of soil microbial community was tested 205 by PERMANOVA with Bray-Curtis dissimilarities and 999 per-mutations. We did not include the 206 spatial location of the plots in data analyses because spatial autocorrelation is not significant using 207 Mantel test.

208 To quantify the relative importance of soil properties and plant community attributes for the soil 209 microbial community composition and carbon-metabolic functions. Variance partitioning analysis 210 was applied for all the plots based on redundancy analysis (RDA) to illus-trate the explanatory power of three matrices including soil physico-chemical properties, plant species diversity, and plant 211 212 functional di-versity (anova.cca function in package vegan). The significance of each explanatory 213 factor was assessed using a permutation test. We further analyzed the correlations between biplot 214 scores from RDA and en-vironmental factors using the functional envfit. In addition, we analyzed the 215 correlations among soil microbial community characteristics, plant community attributes, and soil 216 properties with Spearman correlation. Prior to the above analyses, when the raw data did not meet 217 the nor-mality assumptions, they were log- or sqrt-transformed. The above statistical analyses were

performed in R version 3.4.0 (R Core Team, 2017) using the package vegan (Jari et al., 2013) and
SPSS (version 19.0; SPSS Inc., Chicago, IL, USA).

220 3. Results

221 3.1. Plant community attributes and soil physicochemical properties

The ANOVA showed that all indices of plant community attributes except species richness were significantly changed under different land restoration types. Shannon index and evenness were significantly lower in CF than in the other three land restoration types (Table 1). For the CWMs, the different traits displayed trait-specific responses to land restoration types. SL and CF had a higher CWM for SLA, LNC, LPC, and SRL. SNF and NSF had a higher CWM for LDMC.

Land restoration types had significant effects on soil physicochem-ical properties, except pH (Table
1). Specifically, SWC and SOC were higher in NSF and SNF than in SL and CF. In addition, the soils in
the NSF had a significantly higher TN and TP than the other plant com-munities. The correlation
analysis revealed that there are strong re-lationships among SWC and SOC (P < .01). In addition, the</li>
CWM of SRL was strongly linked to all soil properties except soil pH. Besides of SRL, variation in the
CWM for LDMC and LPC were significantly asso-ciated with SWC, whereas CWM for LDMC and SLA
was tightly corre-lated with SOC (Table 2).

234 3.2. Soil microbial community structure and function

Individual PLFA indicator lipids differed in their response to different land restoration types (Table
3). The NMDs analysis of the PLFAs revealed that land restoration type had a significant effect on
microbial community structure (Fig. 1A, P < .001). The relative abundances of all the microbial</li>
groups except actinomycetes and pro-tozoa were significantly higher in NSF and SNF than in SL and
CF (Table 3).

The ANOVA showed that the carbon-utilization intensity of all compounds except amines
significantly differed across land restoration types (Table 3). The NMDs analysis of the CLPPs
revealed that land restoration type had a significant effect on microbial community carbonmetabolic functions (Fig. 1B, P < .003). Similarly to PLFA, total metabolic activity (indicated by AWCD)</li>
and the utilization intensity of the carbon sources except amines were significantly higher in NSF and
SNF than in SL and CF (Table 3).

247 3.3. Factors determining soil microbial community characteristics

248 The correlation analysis results showed that all the RDA axes of the microbial PLFAs were

significantly linked to the CWM of every trait and the soil properties (SWC and SOC) (Table 4). In

addition, the RDA axes of the microbial CLPPs was tightly correlated with species richness and can

also be explained by the CWM for LDMC, SLA, and SRL (Table 4). Moreover, we also found a

significant correlation between soil micro-bial community composition and carbon-metabolic

253 functions by the permutation test (P < .05, results not shown).

254 Results of variation partitioning showed that plant functional di-versity and soil physicochemical

255 properties cooperatively explained most variation in the soil microbial community composition and

func-tion across land restoration types (Fig. 2). The joint explanations by the two factors were 0.67

and 0.64, respectively. Other factors did not significantly explain the variations in soil microbial

258 community struc-ture and function.

Overall, shifts in the soil microbial community composition across land restoration types occurred in
 parallel with changes in the CWM of traits and soil variables. Changes in soil microbial metabolic
 functions were primarily associated with the CWMs and soil microbial community structure.

262 4. Discussion

263 4.1. Soil microbial community characteristics among land restoration types

264 Soil microbial community composition significantly differed among the four land restoration types 265 (Fig. 1A, Table 3). The total biomass of the soil microbial community was twice as high for SNF and 266 NSF than for SL and CF (Table 3). Some studies have confirmed that this phe-nomenon may be 267 attributed to above ground productivity and litter input because SOC promotes the growth of soil 268 microbes (Gunina et al., 2017; Zhao et al., 2017). In addition, a significant difference for PLFAs was 269 found among land restoration types. With regard to bacterial bio-mass, the greatest abundance of 270 G+ and G- bacteria were found in SNF and NSF, which is consistent with the results of Gunina et al. 271 (2017), who found that there is a greater abundance of G+ and G- bacteria in forest soils than in 272 agricultural soils. The greater abundance of G+ and G- bacteria in NSF and SNF may be linked to the 273 more diverse litter carbon from heterogeneous plant litter inputs (Fierer et al., 2003) and the 274 volume of the rhizosphere due to the increase in plant density (Thoms and Gleixner, 2013),

275 respectively.

276 The reasons for the greater abundance in fungal PLFAs in SNF and NSF can be attributed to both the 277 replacement of species and changes in the microenvironment. The replacement of species with 278 readily de-composable litter by those with more recalcitrant leaf litter can sti-mulate the growth of 279 the fungal biomass (Yannikos et al., 2014). Si-multaneously, most species in SNF and NSF are strongly 280 ectomycorrhizal or arbuscular-mycorrhizal such as plants of the genera Cyclobalanopsis, Quercus, 281 Pinus, and Keteleerla in the study area (Tedersoo and Brundrett, 2017). Moreover, the reduced 282 environmental disturbance in SNF and NSF may also enhance the growth of fungi (Strickland and 283 Rousk, 2010). The increase in actinomycete PLFA content could also be linked to the more 284 recalcitrant leaf litter in SNF and NSF, because actinomycetes may produce enzymes targeting 285 complex and recalcitrant biopolymers (Zhao et al., 2019).

The Biolog EcoPlate data identified potential carbon utilization activities for the soil microbial
community and can be used to assess soil microbial metabolic functions (Liu et al., 2010; Zak et al.,
1994; Zhao et al., 2019). In our research, the CLPP analyses revealed differences among different

land restoration types and showed that the microbial communities in SNF and NSF have a greater potential for utilization of diverse carbon sources compared with SL and CF (Table 3, Fig. 1B). This phenomenon may indicate that there is higher microbial biomass and diversity in SNF and NSF, and furthermore, a greater proportion of the microbial community may be able to utilize diverse carbon com-pounds (Liu et al., 2010; Zhao et al., 2019), which also confirmed by the significant correlation between PLFAs and CLPPs.

4.2. Explanatory factors for soil microbial community among land restoration types

296 We found that the CWMs for plant functional traits are the most important drivers of soil microbial 297 community structure and function (Table 4). The LDMC, as the functional trait for the ratio of 298 structural compounds to the assimilatory issue, represents leaf and litter structural compounds and 299 quality (Cornelissen et al., 2003). The significant po-sitive correlation between the CWM for LDMC 300 and soil microbial community structure and carbon-metabolic functions suggests that an additional 301 carbon source (e.g., cellulose or insoluble sugars) in the litter with higher LDMC improves microbial 302 growth, although some chemi-cally resistant components may decrease the rate of litter decomposi-303 tion (Pei et al., 2016). This explanation is supported by the clear re-lationship between CWM-LDMC 304 and SOC. The SLA, LNC, and LPC are the proxies for litter quality and decomposition rate. Higher 305 values of these functional traits represent higher leaf quality and a more rapid litter decomposition 306 rate, which may lead to a decrease in SOC and soil microbial community composition.

Besides aboveground leaf traits, we also found that the CWM for SRL was not only significantly related to all the soil properties but also to soil microbial community composition and function (Tables 2, 4), which suggests that underground SRL plays a critical role in below-ground ecosystem properties and functions, including the soil microbial community. Recent studies have confirmed that the CWM for root traits explains the variation in microbial parameters related to N cycling better than shoot traits (Legay et al., 2014). Root traits are generally regarded as an indicator of plant resource uptake strategies, soil nu-trient cycling, and root exudate quantity and quality (Bardgett et al., 2014; Cornelissen et al., 2003; Vile et al., 2006). Root litter and root exudates are the
key sources of soil nutrients and energy for microbes. However, we found a negative relationship
between the CWM for SRL and soil microbial community, which suggests that root density or root
biomass could play a more important role due to their effects on the quantity of root litter inputs
and rhizodeposition (Orwin et al., 2010). Therefore, in future research, more root traits should be
examined to explore how roots traits influence the soil microbial community and its impacts on soil
ecosystem processes and functions (Bardgett et al., 2014).

321

322 Many studies have confirmed that soil characteristics, for example, soil pH, SWC, and soil nutrients, 323 play a significant role in shaping the composition of soil microbial communities (Bååth and Anderson, 324 2003; Fierer et al., 2009; Lladó et al., 2018; Stark and Firestone, 1995). In the present study, we only 325 found that SWC and SOC are the key factors, probably due to their influence on soil microbial 326 activities and the fluxes of soil nutrients (Brockett et al., 2012; Stark and Firestone, 1995; Zhao et al., 327 2017). Although some studies have reported soil pH as one of the drivers for soil microbial 328 community composition, we did not find a significant correlation between pH and soil microbial 329 community composition. This may be due to the narrow acidic pH range (4.08–4.26). It is widely 330 recognized that soil nutrients can support and shape the growth and composition of microbial 331 communities (Fierer et al., 2009). It was surprising that soil TN and TP did not play a key role in 332 influencing the soil microbial community in our study. However, we detected significant positive correlations between SOC and the soil microbial community structure. This is consistent with 333 334 previous studies, which showed that changes in SOC induced by aboveground litter input and 335 productivity could shape soil microbial communities by supplying different quality resources for 336 microbial growth (Lladó et al., 2018; Tian et al., 2013; Zhao et al., 2017).

Interestedly, we found that plant functional traits and soil variables cooperatively explained muchmore variation in the soil microbial community than plant functional traits or soil properties alone

(Fig. 2). Together with the significant linkage between CWMs and soil proper-ties, this result
indicates that changes in soil microbial community composition and function can be both the direct
effects of the CWM and the indirect effects due to changes in soil properties. Of the direct ef-fects,
the input and accumulation of diverse litter from plants with different functional attributes supply
complex carbon sources to soil microbes (Liu et al., 2010; Zak et al., 1994). Of the indirect effects,
changes in soil properties (especially SWC and SOC) induced by CWMs simultaneously play a crucial
role in the shaping of soil microbial community.

4.3. Relationships between soil properties and community-weighted mean traits

347 In our study, we found that the CWMs were strongly associated with soil physicochemical properties 348 (Table 2). These results support the mass ratio hypothesis and suggest that soil properties are 349 primarily determined by the functional traits of dominant species. Consistent with our results, many 350 studies have reported that dominant plant traits ex-plain the changes in soil ecosystem functions. 351 For example, Garnier et al. (2004) proposed that functional markers such as SLA, LDMC, and LNC can 352 be used to assess the impacts of community changes on aboveground net primary productivity, litter 353 decomposition, and SOC. In our study, the fast-growth plant species that produce a high quality litter 354 with higher SLA, LNC, LPC, and lower LDMC in SL and CF are typically replaced by slow-growth 355 species producing litter with the opposite characteristics in NSF and SNF (Orwin et al., 2010). 356 Therefore, the higher SOC in NSF and SNF is probably due to two reasons: i) an increase in the rate of 357 litter input and community standing biomass, and ii) a decrease in the rate of litter decomposition. 358 The accumulation of SOC subsequently induced changes in soil TN and TP. We therefore conclude 359 that changes in soil properties across land restoration types primarily contribute to the 360 enhancement of plant productivity and litter biomass due to changes in plant community structure 361 and the re-placement by dominant plant species with different functional traits.

362 5. Conclusions

364 Our results suggest that soil microbial community structure and carbon-metabolic functions significantly differed among land restora-tion types. The significant relationships among the soil 365 366 microbial community, CWMs, and some soil properties suggest that soil microbial community 367 structure and carbon-metabolic functions could be shaped by the functional traits of different 368 dominant plant species and soil properties caused by CWMs. Meanwhile, variance partitioning 369 revealed that plant functional traits and soil variables cooperatively explained 67% and 64% 370 variation in soil microbial community structure and carbon-metabolic functions. Meanwhile, our 371 results imply that natural recovery of forests (NSF and SNF) were better than man-made planta-tion 372 and secondary shrubland in determining soil microbial commu-nities and further developing soil 373 quality.

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- 379 Declaration of Competing Interest
- 380 The authors declare that they have no known competing financial interests or personal relationships
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Table 1 Plant community attributes and soil physicochemical properties in four land restoration types.

	SL		CF	SNF	NSF	F value		
Species diversity indices								
Shannon index Richness	1.85 11.40	± 0.05 a ± 0.56 a	$\begin{array}{l} 1.13 \ \pm 0.12 \ c \\ 10.20 \ \pm 1.32 \ a \end{array}$	$\begin{array}{ll} 1.75 & \pm \ 0.11 \ ab \\ 10.80 & \pm \ 1.11 \ a \end{array}$	$\begin{array}{l} 1.57 \ \pm 0.17 \ b \\ 10.60 \ \ \pm 1.03 \ a \end{array}$	10.11 0.78		
Evenness	0.77	± 0.02 a	$0.49 \pm 0.05 c$	$0.75 \pm 0.04 \text{ ab}$	$0.65 \pm 0.06 \text{ b}$	9.34		
Functional diversity indices								
CWM-LDMC	285.7	± 3.7 c	322.4 ± 7.3 b	395.8 ± 13.6 a	406.8 ± 11.9 a	53.67		
CWM-SLA	13.25	± 0.24 b	17.47 ± 0.58 a	$11.32 \pm 0.61 c$	$9.71 \pm 0.06  d$	61.66		
CWM-LNC	14.02	$\pm 0.18$ a	8.90 ± 0.17 b	8.74 ± 0.14 b	9.22 ± 0.10 b	254.62		
CWM-LPC	0.47	$\pm 0.01$ a	$0.30 \ \pm 0.01 \ b$	$0.28 \ \pm 0.01 \ b$	$0.27 \pm 0.01 \text{ b}$	122.20		
CWM-SRL	38.90	$\pm 0.69 \text{ b}$	44.02 ± 1.12 a	29.26 ± 1.35 c	$18.91 \pm 0.72 \text{ d}$	122.15		
Soil physicochemical properties								
рН	4.15	$\pm 0.14$ a	4.08 ± 0.04 a	4.26 ± 0.01 a	4.19 ± 0.11 a	0.70		
SWC (%)	26.34	$\pm 0.48 \text{ b}$	29.07 ± 1.59 b	31.98 ± 2.37 ab	37.11 ± 2.60 a	5.61		
SOC (mg/g)	28.42	$\pm$ 1.41 b	$26.02 \pm 1.78 \text{ b}$	38.62 ± 3.38 ab	45.11 ± 7.70 a	4.19		
TN (mg/g)	0.48	$\pm \ 0.05 \ b$	$0.44 \ \pm 0.05 \ b$	$0.47 \ \pm 0.05 \ b$	$0.69 \pm 0.06 a$	6.51		
TP (mg/g)	0.25	$\pm 0.00 \text{ b}$	$0.23 \ \pm 0.01 \ b$	$0.22 \pm 0.02 \text{ b}$	$0.34 \pm 0.05 \text{ a}$	4.33		

Values are mean  $\pm$  standard error. Different letters indicate significant differences among land restoration types based on the LSD test (P < .05). \*Significant difference between plant communities based on a one-way ANOVA (\*P < .05 and \*\*P < .01). SL, shrubland; CF, coniferous forest; SNF, semi-natural forest; NSF, natural secondary forest. CWM, community-weighted mean; LDMC, leaf dry matter content; SLA, specific leaf area; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; SRL, specific root length; SWC, soil water content; SOC, soil organic carbon; TN, soil total nitrogen; TP, soil total phosphorus.

Table 2. Correlations between plant community attributes and soil physicochemical properties.

	pH	SWC	SOC	TN	TP
CWM-LDMC	0.24	0.76	0.65	0.19	0.24
CWM-SLA CWM-LNC	-0.35 -0.10	-0.57 -0.53	-0.65 -0.32	-0.50 -0.01	-0.45 -0.01
CWM-LPC	-0.08	-0.69	-0.44	-0.18	-0.15
CWM-SRL	-0.34	-0.73	-0.74	-0.63	-0.58

Asterisks indicate the significance of correlation (P < .05 and P < .01). CWM, community-weighted mean; LDMC, leaf dry matter content; SLA, specific leaf area; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; SRL, specific root length; SWC, soil water content; SOC, soil organic carbon; TN, soil total nitrogen; TP, soil total phosphorus.

	SL	CF	SNF	NSF	F values			
Soil microbial community composition								
Total Biomass (nmol/g)	$11.94\pm0.06\ b$	$14.08\pm0.08\ b$	$21.09 \pm 1.55$ a	$23.90 \pm 1.24 \text{ a}$	32.58			
Bacteria (nmol/g)	$6.33 \pm 0.10 \text{ b}$	$7.92 \hspace{.1in} \pm 0.06 \hspace{.1in} b$	$12.04 \pm 0.95$ a	$13.68 \pm 0.70 \; a$	33.83			
Fungi (nmol/g)	$1.89 \ \pm 0.06 \ b$	$2.03 \hspace{0.2cm} \pm \hspace{0.2cm} 0.06 \hspace{0.2cm} b$	$3.10 \pm 0.16 \ a$	$3.30 \pm 0.29 \ a$	17.56			
Actinomycetes (nmol/g)	$1.00 \pm 0.02 c$	$1.33 \hspace{0.2cm} \pm \hspace{0.2cm} 0.04 \hspace{0.2cm} bc$	$1.63 \hspace{0.2cm} \pm 0.18 \hspace{0.2cm} ab$	1.93 ± 0.11 a	13.68			
AMF (nmol/g)	$0.26 \hspace{0.2cm} \pm 0.00 \hspace{0.2cm} c$	$0.31 \hspace{0.2cm} \pm \hspace{0.2cm} 0.01 \hspace{0.2cm} c$	$0.47 \ \pm 0.04 \ b$	$0.56 \hspace{0.2cm} \pm 0.02 \hspace{0.2cm} a$	43.73			
Protozoa (nmol/g)	$0.04 \pm 0.00 \ b$	$0.03 \hspace{0.2cm} \pm \hspace{0.2cm} 0.00 \hspace{0.2cm} b$	$0.08 \hspace{0.2cm} \pm 0.01 \hspace{0.2cm} ab$	$0.13 \pm 0.04 \ a$	5.39			
G+ (nmol/g)	$2.30 \hspace{0.2cm} \pm \hspace{0.2cm} 0.05 \hspace{0.2cm} b$	$2.73 \hspace{0.2cm} \pm \hspace{0.2cm} 0.05 \hspace{0.2cm} b$	$3.72 \pm 0.32 a$	4.27 ± 0.25 a	19.03			
G- (nmol/g)	$3.21 \pm 0.12 c$	$4.34\pm0.01~b$	$7.18 \pm 0.55 \ a$	8.27 ± 0.39 a	47.16			
Fungi/Bacteria	$0.30 \ \pm 0.01 \ b$	$0.26 \hspace{0.2cm} \pm \hspace{0.2cm} 0.01 \hspace{0.2cm} ab$	$0.26 \hspace{0.2cm} \pm 0.01 \hspace{0.2cm} ab$	$0.24 \pm 0.02 \ a$	3.11			
G+/G-	$0.72 \pm 0.04 \ a$	$0.63 \hspace{0.2cm} \pm \hspace{0.2cm} 0.01 \hspace{0.2cm} b$	$0.52 \hspace{0.2cm} \pm 0.00 \hspace{0.2cm} c$	$0.52 \hspace{0.2cm} \pm 0.02 \hspace{0.2cm} c$	22.03			
Community-level physiological profiles								
AWCD	$0.37 \pm 0.13 \text{ bc}$	$0.22 \hspace{0.2cm} \pm 0.03 \hspace{0.2cm} c$	$0.67 \pm 0.07 \ a$	$0.60 \hspace{0.2cm} \pm 0.08 \hspace{0.2cm} ab$	5.89			
Carboxylic acids	$0.50 \pm 0.04 \ b$	$0.28 \hspace{0.2cm} \pm 0.04 \hspace{0.2cm} c$	$0.81 \pm 0.09 \ a$	$0.52 \hspace{0.2cm} \pm 0.06 \hspace{0.2cm} b$	13.01			
Polymers	$0.49 \pm 0.12 \ b$	$0.61 \hspace{0.2cm} \pm \hspace{0.2cm} 0.07 \hspace{0.2cm} b$	$0.73 \pm 0.06 \ ab$	$0.90 \pm 0.04 \ a$	4.97			
Carbohydrates	$0.42 \pm 0.10 \text{ bc}$	$0.21 \pm 0.03 c$	$0.64 \hspace{0.2cm} \pm 0.07 \hspace{0.2cm} ab$	$0.72 \pm 0.10 \ a$	8.90			
Phenolic acids	$0.18 \pm 0.09 \ b$	$0.14 \hspace{0.1in} \pm 0.09 \hspace{0.1in} b$	$0.46 \pm 0.16 a$	$0.65 \pm 0.03 \ a$	5.71			
Amino acids	$0.22 \hspace{0.2cm} \pm 0.06 \hspace{0.2cm} b$	$0.20 \hspace{0.2cm} \pm 0.04 \hspace{0.2cm} b$	$0.58 \pm 0.06 \ a$	$0.73 \pm 0.16 \ a$	8.43			
Amines	0.20 ± 0.10 a	$0.15 \ \pm 0.04 \ a$	$0.20 \pm 0.07 \ a$	$0.37 \pm 0.15 \ a$	0.99			

Table 3. Soil microbial community composition and community-level physiological profiles in four land restoration types.

Values are mean  $\pm$  standard error. Different letters indicate significant differences among land restoration types based on the LSD test (P < .05). Significant difference between plant communities based on a one-way ANOVA (P < .05 and P < .01). SL, shrubland; CF, coniferous forest; SNF, semi

Variables	PLFA				CLPP				
	RDA1	RDA2	r <sup>2</sup>	Р	RDA1	RDA2	r <sup>2</sup>	Р	
Species diversity indices									
Shannon index	0.054	-0.999	0.362	0.136	-0.467	0.884	0.397	0.100	
Richness	0.824	-0.567	0.438	0.077	-0.841	0.541	0.554	0.026	
Evenness	-0.299	-0.954	0.282	0.213	-0.200	0.980	0.211	0.351	
Functional diversity indices	Functional diversity indices								
CWM-LDMC	0.998	0.015	0.758	0.002	-0.996	0.089	0.544	0.034	
CWM-SLA	-0.764	0.645	0.833	0.001	0.992	-0.126	0.677	0.006	
CWM-LNC	-0.737	-0.676	0.731	0.002	0.797	0.604	0.223	0.300	
CWM-LPC	-0.854	-0.520	0.763	0.002	0.859	0.511	0.336	0.178	
CWM-SRL	-0.908	0.419	0.899	0.001	0.983	0.183	0.809	0.001	
Soil physicochemical properties									
рН	0.950	-0.313	0.129	0.519	-0.987	0.161	0.216	0.330	
SWC	0.986	0.168	0.742	0.006	-0.884	-0.467	0.297	0.223	
SOC	0.999	0.044	0.715	0.005	-0.946	-0.323	0.271	0.264	
TN	0.736	-0.677	0.422	0.096	-0.726	-0.688	0.419	0.091	
ТР	0.994	-0.105	0.299	0.216	-0.425	-0.905	0.324	0.172	

Table 4. Significance analysis of correlation between the redundancy analysis (RDA) axes of microbial community properties (PLFA and CLPP) and indices of species diversity, functional traits, and soil properties.

 $r^2$  represents the proportion of variance explained. Asterisks indicate the significance of correlation based on Monte Carlo permutation test (n = 999). P < .05, P < .01, P < .001. CWM, community-weighted mean; LDMC, leaf dry matter content; SLA, specific leaf area; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; SRL, specific root length; SWC, soil water content; SOC, soil organic carbon; TN, soil total nitrogen; TP, soil total phosphorus.



Fig. 1. Non-metric multidimensional scaling (NMDs) analysis of (A) soil mi-crobial community composition and (B) soil microbial carbon-metabolic functions within soils across land restoration types (the distance metric was the Bray-Curtis metric). The same shapes represent three replicates of the twelve plots of this study. The significance test was based on a PERMANOVA.